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Marine Migration and Natural Mortality of North American Atlantic Salmon (Salmo salar L.)

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TABLE OF CONTENTS

TABLE OF CONTENTS	iii
LIST OF TABLES.....	v
LIST OF FIGURES	viii
PREFACE	ix
ABSTRACT/RESUME	x
1.0 INTRODUCTION	1
2.0 MARINE MIGRATIONS	3
2.1 INTRODUCTION	3
2.2 LITERATURE REVIEW	3
2.3 ANALYSES AND RESULTS	7
<u>2.3.1 Migration routes</u>	7
2.3.1.1 Post-smolt migrations	8
2.3.1.2 Feeding and return migrations	10
2.3.1.3 Previous spawner migrations	11
2.3.1.4 Comparison of return migrations of previous spawners and 2SW salmon ..	13
<u>2.3.2 Variation in latitudinal distribution</u>	13
2.3.2.1 In Newfoundland fishery	13
2.3.2.2 In Northwest Atlantic	14
<u>2.3.3 Temperature effects on distribution</u>	16
2.3.3.1 In Newfoundland fishery	16
2.3.3.2 In Northwest Atlantic	16
2.4 DISCUSSION	17
2.5 CONCLUSIONS	22
3.0 MARINE NATURAL MORTALITY	22
3.1 INTRODUCTION	22
3.2 LITERATURE REVIEW	23
3.3 ANALYSES AND RESULTS	32

<u>3.3.1 Natural mortality between smolt and recruitment</u>	32
3.3.1.1 Salmon of Big Salmon River	32
3.3.1.2 Salmon of Sand Hill River	35
<u>3.3.2 Natural mortality between spawnings</u>	36
3.3.2.1 Spawners of Big Salmon River	36
3.3.2.2 Spawners of LaHave River	37
<u>3.3.3 Smolt survival and migration time</u>	39
3.3.3.1 Wild smolts	39
3.3.3.2 Hatchery smolts	40
<u>3.3.4 Failure of the 1977 smolt class</u>	41
<u>3.3.5 Effects of marine temperature on recruitment</u>	43
3.3.5.1 Upper Bay of Fundy salmon	43
3.3.5.2 Western Arm Brook salmon	46
<u>3.3.6 Effects of forage availability on recruitment</u>	47
<u>3.3.7 Effects of predation on recruitment</u>	49
3.3.7.1 Cormorants	49
3.3.7.2 Cod and grey seals	50
3.4 DISCUSSION	52
3.5 CONCLUSIONS	61
4.0 ACKNOWLEDGEMENTS	62
5.0 REFERENCES	63
6.0 TABLES	82
7.0 FIGURES	131

LIST OF TABLES

1a.	Location and time of recovery as post-smolts from tagged wild and native hatchery smolts emigrating from Big Salmon River, New Brunswick, 1967 to 1973	82
1b.	Location and time of recovery as post-smolts from tagged hatchery smolts emigrating from Lower Fundy and Gulf of Maine rivers	83
1c.	Location and time of recovery as post-smolts from tagged hatchery smolts emigrating from rivers in southwest Nova Scotia, 1971 to 1984	84
1d.	Location and time of recovery as post-smolts from tagged wild and hatchery smolts emigrating 1959 to 1982, from rivers emptying into the Gulf of St. Lawrence, i.e., Margaree River and River Philip, Nova Scotia, Miramichi River, New Brunswick, and several Quebec rivers grouped according to geographic areas of the Gaspé, Anticosti Island and Upper North Shore	85
2a.	Location and time of recovery as 1SW and 2SW salmon at mouth of home river and in the sea from tagged wild and native hatchery smolts emigrating from Big Salmon River, 1967 to 1973	88
2b.	Location and time of recovery as 1SW and 2SW salmon at mouth of home river and in the sea from tagged native hatchery smolts released into the Saint John River, 1967 to 1984	89
2c.	Location and time of recovery as 1SW and 2SW salmon at mouth of home river and in the sea from tagged hatchery smolts released into the LaHave River, 1971 to 1984	91
2d.	Location and time of recovery as 1SW and 2SW salmon at mouth of home river and in the sea from tagged wild smolts emigrating from the Miramichi River, 1968 to 1976	93
3a.	Location and time of recovery as previous spawners at mouth of home river and in the sea for maturing salmon of Saint John River, tagged in river during preceding spawning migrations, 1967 to 1983	95
3b.	Location and time of recovery as previous spawners at mouth of home river and in the sea for maturing salmon of Miramichi River, tagged in river during preceding spawning migrations, 1967 to 1981	97

4.	Annual variation in northward distributions of commercial catches of small (<2.7 kg) and large (≥2.7 kg) salmon along east and south coasts of insular Newfoundland, 1969 to 1984.....	99
5a.	Annual variation in the northward distributions of recaptures from tagged wild smolts of Miramichi River recovered as 1SW and 2SW salmon along east and south coasts of insular Newfoundland.....	100
5b.	Annual variation in the northward distributions of recaptures from tagged hatchery smolts of Saint John and LaHave rivers recovered as 1SW salmon along east and south coasts of insular Newfoundland.....	101
6.	Results of variance test for homogeneity of proportions of salmon catches and tag recaptures along east and south coast of insular Newfoundland made in northern Areas A and B.....	101
7.	Numbers and proportions of tag recaptures as 1SW salmon in Newfoundland-Labrador fishery and at Greenland from native hatchery smolts released into Saint John River..	102
8.	Index of spring SST along the east coast of Newfoundland, 1969 to 1984.....	103
9.	Regression coefficients and their significance for linear comparisons of proportions of salmon caught or recaptured in Areas A and B, Newfoundland, on Julian day that 0°C isotherm receded north of 50°N.....	103
10.	Indices of SST in Labrador Sea and along west coast of Greenland, 1970 to 1984.....	104
11.	Numbers of virgin salmon, categorized by sea age, returning to Big Salmon River, 1967 to 1973.....	105
12.	Location, method and sea age of tag recaptures from 30542 wild smolts of Big Salmon River, 1967 to 1971.....	106
13.	Survival and natural mortality rates for untagged smolts of Big Salmon River, 1966 to 1971.....	107
14.	Distributions of recaptures and catches from tagged and untagged smolts of Sand Hill River, 1969 to 1971.....	108
15.	Survival and natural mortality rates for untagged smolts of Sand Hill River, 1969 to 1971.....	109
16.	Returns of maturing salmon by sex and sea age to Big Salmon River, 1968 to 1972.....	110

17.	Mortality between spawning and subsequent return to Big Salmon River.....	112
18.	Mortality between spawning and subsequent return to Big Salmon River according to sex and number of spawnings..	113
19.	Estimates of grilse (<63 cm) and large salmon (≥63 cm) returning to the LaHave River from wild smolts produced above Morgan Falls, New Germany.....	114
20.	Sample aging data for wild salmon passed through counting trap at Morgan Falls, LaHave River.....	115
21.	Mortality between spawning and subsequent return to river for wild salmon of upper LaHave River.....	116
22.	Five years of Miramichi River smolt tagging and recapture data with tagging dates and minimum water temperatures (°C).....	117
23.	Results of weighted regression analyses of tag recapture rate for wild smolts on tagging date and minimum estuarial temperature, Miramichi River.....	119
24.	Tagging and recapture data with release dates for thirteen groups of hatchery smolts released into LaHave River, 1978 to 1981.....	119
25.	Nominal catches and anomalies to base-year catches for small and large salmon harvested in 1978 and 1979, respectively.....	120
26.	Recreational catches of grilse and surrogates of mean flows during main fishing periods for Big Salmon and Stewiacke rivers, and mean SST in Bay of Fundy during June-July of post-smolt year (SST).....	124
27.	Counts of smolts and resultant returns of 1SW salmon to Western Arm Brook and numbers of 1SW salmon harvested in Area N commercial fishery from smolt classes 1971 to 1983.....	126
28.	Comparisons of sea growth for hatchery and wild smolts emigrating from LaHave River in 1977, 1978 and 1980....	127
29.	Comparison of summer-fall growth rate in first sea-year for 1977 smolt class with comparable rates for 1976 and 1978 to 1986 smolt classes.....	128

30.	Numbers and potential sources of salmon tags recovered from cormorant rookeries on Tobacco and Indian islands, Nova Scotia.....	129
31.	Recreational catches of grilse for selected rivers or areas, 1972 to 1986.....	130

LIST OF FIGURES

1.	Maps of northwest Atlantic (1a) and northeast North America (1b) showing locations of areas and sites referenced in text.....	131
2.	Plots of percent tag recaptures for wild smolts of the Miramichi River against tagging date (i.e., time of migration).....	132
3.	Plot of percent tag recaptures for hatchery smolts against release date.....	133
4.	Relationships between indices of 1SW salmon production for populations of Big Salmon and Stewiacke rivers and Mean SST in the Bay of Fundy during June-July of post-smolt year (SST).....	134
5.	Relationships between percent survival (expressed as number of recruits per 100 smolts) for smolts of Western Arm Brook and indices of winter SST conditions in the northwest Atlantic.....	135
6.	Locations of Tobacco and Indian islands, the sites of two cormorant rookeries, and nearby rivers into which tagged hatchery smolts were released, 1981 to 1986.....	136

PREFACE

This manuscript was submitted August, 1989, to Dalhousie University, Halifax, Nova Scotia, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

Ritter, John A. 1989. Marine migration and natural mortality of North American Atlantic salmon (*Salmo salar* L.). Can. MS. Rep. Fish. Aquat. Sci. No. 2041. 136 p.

Marking and field sampling data, and catch statistics are used to describe migrations of North American Atlantic salmon (*Salmo salar* L.) and to quantify and explain variations in marine natural mortality. Sea distributions fall into two population groupings; upper Bay of Fundy salmon limit their migrations to the Bay of Fundy area while other populations migrate to and from the northwest Atlantic east of Newfoundland. Sea surface temperatures (SST) affect migration patterns and influence catch distribution and rate. Survival rates from smolt to recruitment average more than 20% for salmon of Sand Hill River, Labrador, and less than 10% for the upper Bay of Fundy population of Big Salmon River, New Brunswick. Losses to natural mortality between spawnings are greater among males, increase with number of spawnings and are lower for salmon of upper Bay of Fundy rivers than for other populations. Smolts passing through the estuary early or late in the migration period experience lower survival. Factors affecting recruitment are capable of widespread effects as indicated by low survival rates for the 1977 smolts of many rivers from Maine to southern Labrador. Reduced grilse catches on upper Bay of Fundy rivers are associated with warmer June-July SST in the western Bay of Fundy. Variable recruitment rates for smolts of Western Arm Brook, Newfoundland, seem linked to the northward extent of warm winter SST in the northwest Atlantic. Possible scarcity of forage did not cause starvation of the 1977 smolt class, but may have affected species interactions and post-smolt predation. Predation by double-crested cormorants (*Phalacrocorax auritus*) is site specific, varies annually, and is probably different for hatchery and wild salmon. Recruitment success, while annually variable, is unchanged since the early 1970s, and seems unaffected by recent increases in abundances of cod (*Gadus morhua*) and grey seals (*Halichoerus grypus*).

RÉSUMÉ

Ritter, John A. 1989. Marine migration and natural mortality of North American Atlantic salmon (*Salmo salar* L.). Can. MS. Rep. Fish. Aquat. Sci. No. 2041. 136 p.

Les données de marquage et d'échantillonnage sur place ainsi que les statistiques de prises servent à établir les migrations du saumon de l'Atlantique nord-américain (*Salmo salar* L.) et à quantifier et expliquer les variations dans la mortalité naturelle de ce poisson en milieu marin. En mer, les saumons se concentrent en deux groupes de populations; celui de la partie supérieure de la baie de Fundy limite ses migrations à la baie de Fundy, tandis que les autres populations évoluent dans le nord-ouest de l'Atlantique, à l'est de Terre-Neuve. Les températures superficielles de la mer affectent les habitudes migratoires et influent sur le taux de prises et sur la distribution de ces dernières. Les taux de survie depuis l'état de saumonnette à celui où le poisson est recruté à la pêche s'établissent en moyenne à plus de 20 p. 100 pour le saumon de la rivière Sand Hill (Labrador) et à moins de 10 p. 100 pour le saumon de la rivière Big Salmon (Nouveau-Brunswick), lequel appartient à la population de la partie supérieure de la baie de Fundy. La mortalité naturelle parmi les reproducteurs est plus grande chez les mâles et croît avec le nombre de fraies; elle est plus basse chez les saumons des rivières se jetant dans la partie supérieure de la baie de Fundy que chez les saumons des autres populations. Les saumonnettes qui traversent l'estuaire au début ou à la fin de la période de migration connaissent un taux de survie plus faible que les autres. Les facteurs influençant le recrutement peuvent avoir de vastes répercussions, comme l'ont révélé les faibles taux de survie enregistrés en 1977 parmi les saumonnettes de nombreuses rivières, depuis le Maine jusqu'au sud du Labrador. La diminution des prises de saumonnettes dans la partie supérieure de la baie de Fundy est reliée à la hausse de la température superficielle de la mer dans l'ouest de la baie de Fundy en juin-juillet. La variabilité des taux de recrutement des saumonnettes dans le ruisseau Western Arm (Terre-Neuve) semble due à une progression vers le nord des chaudes températures superficielles hivernales des eaux de l'Atlantique nord-ouest. La rareté possible de la nourriture n'a pas causé de famine parmi les saumonnettes de la classe 1977, mais a pu affecter les interactions entre espèces et la prédation au stade de post-saumonnette. La prédation par les cormorans à aigrettes (*Phalacrocorax auritus*) est propre à certains endroits, varie annuellement et diffère probablement pour les saumons d'élevage et les saumons sauvages. Le recrutement, quoique variable d'une année à une autre, n'a pas changé depuis le début des années 1970, et ne semble pas touché par les accroissements récents de l'abondance de morue (*Gadus morhua*) et de phoque gris (*Halichoerus grypus*).

1.0 INTRODUCTION

The present natural breeding range of the anadromous Atlantic salmon (Salmo salar L.) in North America extends from the Pawcatuck River in Rhode Island (42°N) (Anon. 1985a) to Ungava Bay, Quebec (58°N) (MacCrimmon and Gots 1979). Within this range there are more than 500 rivers which collectively support an annual production of more than 1.0 million recruits (Ritter et al. 1979a). Wild and hatchery stocks of the United States produce fewer than 20,000 recruits annually (Anon. 1985a).

The freshwater residency time of the anadromous form of the North American Atlantic salmon mainly varies from two to seven years depending upon the length of the growing season (Power 1981). Salmon greater than 15-20 g by late spring leave the rivers (Pratt et al. 1974; Jessop 1975; Chadwick 1981) and according to tagging studies migrate to feeding areas east of Newfoundland and Labrador (Ritter 1972; Tetreault and Carter 1972; Pratt et al. 1974; Turner 1975b; Meister 1984). Salmon destined to mature as two-sea-winter (2SW) and older salmon have been recorded as far north as Disko Bay, Greenland (70°N) (Jensen 1980; Ruggles and Ritter 1980). Maturing fish first return to their rivers of origin to spawn after one, two and occasionally three and four years following their initial departure from fresh water.

North American Atlantic salmon are harvested in coastal fisheries along their feeding and return migration routes and in their native rivers. The mean annual recorded catch of Atlantic salmon in North American fisheries from 1970 to 1984 is 2061 tonnes (Anon. 1986b) or roughly 650,000 fish. The North American catch represents about one sixth the world catch of anadromous Atlantic salmon (Anon. 1979, 1986b). Canadian fisheries (i.e., commercial, Indian food and recreational) account for almost all of the North American catch; USA catch ranged from 0.9 to 6.4 tonnes since 1970 (Anon. 1986b). Salmon from North American rivers also comprise roughly 50% of the catch off the west coast of Greenland (Anon. 1986b). During the peak of the Greenland fishery (i.e., 1969-75), and prior to the implementation of quotas, catches generally exceeded 2000 tonnes (Anon. 1986b).

The Canadian harvest of Atlantic salmon is regulated to ensure a sustained yield from the resource and an equitable sharing of it among resource users. The first of these objectives is based on biological assessments for individual stocks or their groupings. Ideally there are two components to these assessments: (i) estimates of spawning requirements to fully seed the accessible freshwater habitat; and (ii) forecasts of the returns of one-sea-winter (1SW) and multi-sea-winter (MSW) salmon to the home river. The assessments provide a biological basis for the definition of total allowable catches for

populations of a few large river systems (e.g., Restigouche, Miramichi and Saint John rivers, New Brunswick) and assignment of quotas or seasons, or both, for the various fisheries. The detailed nature of assessments varies, depending largely upon availability and accuracy of biological information. Annual forecasts of adult returns to river systems and areas are flawed by assumptions that marine mortality rates for fishing and attributed to natural causes are constant (Marshall 1985; Chadwick and Peppar 1985; Cutting and Jefferson 1985; Randall et al. 1985a, 1986).

The different life stages of the salmon are designated according to the system of terminology adopted by the International Council for the Exploration of the Sea, i.e., ICES (Allan and Ritter 1977). Most confusing of the terminology are the different terms to refer to salmon that have spawned (e.g., kelt, post-spawners, previous spawners) and the designations of sea age based on fish size. Salmon that have spawned are designated as previous spawners regardless of the elapsed time since the initial spawning. Salmon designated small and large are assumed to be comprised of 1SW and 2SW salmon, respectively. The large salmon category also includes the 3SW salmon and most of the previous spawners. The term grilse refers to small salmon that are maturing.

Salmon biology data used herein were extracted from central files of the Department of Fisheries and Oceans of Canada (DFO), collected through ongoing DFO programs, developed from scale samples available within DFO, and obtained from colleagues and various publications. Data were analyzed using the Minitab statistical package. Minitab was selected because its interactive capabilities facilitated data manipulation and programming of statistical routines.

Locations of sites and areas identified in text are given in Fig. 1.

The thesis is divided into two sections. The first describes marine migrations of North American salmon while the second pertains to their natural mortality in the sea. The two subjects were assumed to be related since losses to natural mortality were expected to vary with sea distribution. Investigations were aimed at confirming theories and suggestions advanced in the literature and at exploring new relationships that would enhance understanding of the marine phase of the life cycle.

2.0 MARINE MIGRATIONS

2.1 INTRODUCTION

Understanding of marine migration routes of North American Atlantic salmon is based largely on results of tagging studies involving hatchery-reared and wild smolts (Ritter 1972; Tetreault and Carter 1972; Pratt et al. 1974; Turner 1975a, 1975b; Jessop 1976; Caron 1983; Meister 1984) and 1SW and older salmon marked in the river (Turner 1975b; Meister 1984) or at sea (Belding and Prefontaine 1938; Belding 1940; Blair 1956, 1957a, 1957b; Reddin and Burfitt 1984). About 4.0 million salmon (98% smolts) have been marked with dangler tags by American and Canadian fisheries agencies since the mid-1960s (Anon. 1981, 1985c; unpub. data). Although these studies have produced numerous recaptures in the sea, descriptions of migration routes are sketchy because of the scarcity of recaptures as post-smolts (i.e., salmon in their first year at sea) and the absence of recaptures during late fall to spring months when exploitation of salmon in the sea is nil. Further problems are that most data series are either not reported or the condensed format under which they are reported limits their usefulness in comparisons.

Tag recapture data for selected populations are used to depict the sea migration of North American salmon of different sea ages. Annual variations in the distributions of salmon catches along the Newfoundland coast and between Newfoundland and Greenland are described relative to sea surface temperatures (SST).

2.2 LITERATURE REVIEW

Salmon from rivers of the USA, Maritime Provinces and Quebec migrate northeast to areas east of Newfoundland (Pippy 1982; Meister 1984). Some potential MSW salmon extend their migrations to the Davis Strait area where they contribute to the fishery off West Greenland (Ruggles and Ritter 1980). Tagged salmon from American and Canadian rivers have also been recaptured near Angmagssalik, East Greenland (Jensen and Lear 1980). Non-maturing 1SW salmon from a single population are widely dispersed throughout the northwest Atlantic. According to tag recaptures they are present in July-September both at Greenland and along the Newfoundland-Labrador east coast (Turner 1975b; Ruggles and Ritter 1980; Pippy 1982; Meister 1984).

The outbound migrations of salmon from rivers in Maine, USA, are east and northward along the Atlantic coast of Nova Scotia (Meister 1984). Post-smolt recaptures in Newfoundland statistical areas I and J (13 of 259 post-smolt recaptures) confirm a migration to the southwest tip of Newfoundland (Meister

1984). The migration route east and north of this point for salmon of this southern population remains unknown since no recaptures of post-smolts were reported in areas either eastward along the south coast or northward along the west coast of Newfoundland. Post-smolts originating from Quebec rivers that drain into the Gulf of St. Lawrence, exit the Gulf through the Strait of Belle Isle and the Cabot Strait (Caron 1983).

Return migrations vary in relation to population origin. Results of smolt tagging studies indicate that salmon returning to rivers in Maine generally avoid the fisheries along the Atlantic coasts of Newfoundland and Nova Scotia in their maturing year (Meister 1984). In contrast, maturing 1SW and older salmon enroute to rivers along the Atlantic coast of Nova Scotia and emptying into the Gulf of St. Lawrence are harvested along the east and south coasts of Newfoundland in their maturing year (Blair 1956; Ritter 1972; Turner 1975b; Pippy 1982). Similarly, recaptures of salmon from North Harbour River, St. Mary's Bay, Area G, Newfoundland, indicate a return migration in their maturing year from the northwest Atlantic along the east coast of insular Newfoundland (Lear and Day 1977). Tagged smolts of the Sand Hill River, southern Labrador (Pratt et al. 1974), and the Exploits River, Area B, Newfoundland (O'Connell et al. 1985), are generally recaptured in their maturing year about and south of their respective river mouths.

Results of marine tagging studies suggest that fish homing to Gulf rivers return by both the Cabot Strait and the Strait of Belle Isle (Belding 1940; Blair 1956, 1957a, 1957b; May 1973; Reddin and Burfitt 1984). Belding (1940) concluded from recaptures for fish tagged at St. Anthony, Area A, Newfoundland, and Port-aux-Basques, Area J₂, Newfoundland, that salmon homing to rivers on the north shore of Quebec, east of the Natashquan River (62°W), and on the west coast of Newfoundland, north of Bay of Islands (49°N), return by the Strait of Belle Isle, and that salmon returning to more western and southeastern parts of the Gulf utilize the Cabot Strait.

Time of return migrations for maturing salmon from east of Newfoundland varies with sea age (Pippy 1982). MSW salmon approach the coast of Newfoundland first and are earlier than 1SW salmon by two weeks or more (Turner 1975b; Pippy 1982). Returns to home rivers display a similar trend (Saunders 1967; O'Neil and Swetnam 1984; Swetnam and O'Neil 1984).

The outbound migration routes of previous spawners of the Miramichi River, New Brunswick (Turner 1975b), and the Little Codroy River, Area K, Newfoundland (Murray 1958), are inconsistent with return migration routes indicated by recaptures from smolt marking studies (Murray 1958; Turner 1975b). Previous spawners from both rivers were reported recaptured along the

Newfoundland west coast and in or near the Strait of Belle Isle. Recaptures of marked smolts homing to both the Miramichi and Little Codroy rivers indicate return migrations by the south coast of Newfoundland and the Cabot Strait (Murray 1958; Turner 1975b).

A possible exception to outbound migrations of North American salmon culminating to the east of Newfoundland is the migration of salmon from Big Salmon River, New Brunswick. Jessop (1976) reported that all but one of 178 recaptures from tagged wild smolts of this river were made within the Bay of Fundy and the home river. The single sea recapture outside the Bay of Fundy was a 2SW salmon reported caught in Area J₂, Newfoundland.

Known rates of travel for salmon in the sea have been documented through tagging studies. Meister (1984) reported an average travel speed for post-smolts from Maine to the southwest tip of Newfoundland of about 24 km/day. Montevecchi et al. (1988), based on seven tags found in a seabird colony on Funk Island, Area B, Newfoundland, computed an average travel speed for post-smolts from Maine of 19.5 km/day. Blair (1956) reported average travel speeds of 35 and 22 km/day for grilse and large salmon marked in Bonavista Bay, Area C, Newfoundland, and recaptured in coastal fisheries and rivers of Quebec and the Maritime provinces. Maximum rates reported by Blair (1956) for grilse and large salmon were 52 and 42 km/day. In analyses of interceptions of mainland salmon in the Newfoundland-Labrador fishery, an average travel rate of 32 km/day was assumed for maturing salmon of all sea ages (Pippy 1982). This rate was also based on an analysis of data from marine tagging studies. Meister (1984) reported a rate of 26 km/day for Maine previous spawners migrating to Newfoundland and Greenland.

Travel rates determined from tagging data are conservative estimates of swimming speed since current speed is not considered and it is unlikely that salmon travel continuously or in a direct path. The average travel rate reported by Meister (1984) for post-smolts from Maine rivers (about 24 km/day) is about half their sustained swimming capability (i.e., at least two body lengths/sec according to Stasko et al. 1973). The average travel rates reported by Blair (1956) for grilse (35 km/day) and maturing large salmon (22 km/day) are also considerably less than their swimming capabilities.

Migrations of salmon cannot be attributed to passive drift as travel speeds are generally greater than current velocities and often passage is against the current (Stasko et al. 1973). Recaptures from salmon tagged in the river (Ritter 1972; Pratt et al. 1974; Turner 1975b; Caron 1983) and in the sea (Belding and Prefontaine 1938; Belding 1940; Blair 1956, 1957a, 1957b; Reddin and Burfitt 1984) display no evidence that sea migration routes

are determined by ocean currents.

Precision of homing of North American salmon was investigated by Stasko et al. (1973) in their review of recapture data for tagged and finclipped smolts emigrating from Canadian rivers between 1950 and 1970. Considering recaptures in both fresh water and the sea, only 6 of 8314 (<0.1%) were made in a river other than the one from which salmon migrated as smolts. Among the recaptures in fresh water, 5 of 6565 (<0.1%) were in the wrong river. For Swedish salmon, Carlin (1968) reported stray rates of about 2% for salmon feeding in the Baltic Sea and less than 1% for salmon from Sweden's west coast rivers. Although Hansen and Lea (1982) report higher rates of straying into the wrong river for tagged groups of Norwegian salmon (i.e., 2.5 to 17.6% of freshwater recaptures), their results are atypical (Anon. 1983). Most smolt tagging studies indicate precise homing to the river from which salmon emigrate as smolts.

Stasko et al. (1973) estimated straying of North American salmon in salt water to be 2.2% of all recaptures. This rate however, was derived assuming that all fish pass by insular Newfoundland on their outbound and return migrations. The majority of these strays were salmon from rivers draining into the Gulf of St. Lawrence which were recaptured along the Atlantic coast of Nova Scotia and in the Bay of Fundy. These fish may have been following alternative feeding and return migration routes rather than being lost.

Recently, two recoveries from tagged hatchery smolts released into the Liscomb River, Nova Scotia, were made in the Faroese longline fishery in the Norwegian Sea (Reddin et al. 1984; Reddin 1987). Tags of two other salmon marked as smolts in North America were previously returned from Norway (Reddin et al. 1984; Reddin 1987). Unlike the two recaptures in the Faroese fishery, which were verified through the information returned with the tags, the two recaptures from Norway were returned with conflicting and no information, respectively. The status of these transatlantic migrants as either lost at sea or on alternate migration routes which would have returned them to their home rivers, is unknown. Regardless, the number (i.e., two or possibly four recaptures) is negligible considering that smolts tagged in North America since 1970 have yielded more than 15,000 recaptures as 1SW and MSW salmon (Anon. 1981, 1985c; unpub. data).

A main factor affecting the sea distribution of salmon is water temperature. Catch rates at West Greenland are reported to vary in relation to SST (Christensen and Lear 1980; Reddin and Shearer 1987). May (1973), in his description of the distribution of salmon in the northwest Atlantic, reported salmon to be found generally in 3 to 6°C surface waters east of the

Canadian shelf from northern Labrador to the southern Grand Bank. He reported very few salmon were caught during test fishing in waters at 2°C or less. Reddin and Burfitt (1984) reported a direct correlation between catch rate (CPUE) in spring and SST in the area of the Grand Bank.

Low sea temperatures in January and August in the northwest Atlantic were identified through a multiple linear regression approach as being partly responsible for the low abundances of salmon at West Greenland in 1983 and 1984 (Anon. 1985b; Reddin and Murray 1985; Reddin and Shearer 1987). Cold sea temperatures are thought to have inhibited the movement of salmon northward in the Davis Strait and along the Greenland coast.

Salmon distribution and catches in coastal waters of Newfoundland are also assumed to be influenced by local sea temperature conditions in spring (Pippy 1982; O'Connell et al. 1985). Reddin and Shearer (1987) reported MSW salmon recaptures from tagged smolts of the Sand Hill River to be distributed further south along the east coast of Newfoundland when the 4°C surface isotherm for June was farthest south. This evidence must be viewed as preliminary because recapture data were available for only three years and recaptures made as 1SW salmon did not show a similar pattern. Reddin and Shearer (1987) speculated that 1SW salmon returning to the Sand Hill were not affected because their migration into coastal water is a month later, by which time the 4°C surface isotherm has receded north of the Sand Hill.

The spatial distribution of salmon in the sea may also vary in relation to the distribution of prey species. Christensen and Lear (1980) reported a positive relationship between salmon catch at West Greenland and stomach content weight. Reddin (1985) reported from surveys conducted in May 1979 and 1980 that salmon were more abundant in the oceanic areas east of the Grand Bank than over the Bank even though those over the Bank had more food in their stomachs. Reddin (1985) noted that 5 to 8°C temperatures were more prevalent in the oceanic areas than over the Bank. This may imply that temperature influences distribution more than food availability.

2.3 ANALYSES AND RESULTS

2.3.1 Migration Routes

Temporal and spatial distributions of salmon in the sea were investigated through recaptures of tagged salmon marked in their home river as smolts and 1SW and older salmon. Tag recaptures are summarized by sea age, spawning history and area and month of recapture. Recaptures as post-smolts represent the outbound

migrations of salmon from their native rivers. The feeding and return migrations are illustrated by sea recaptures as 1SW and older salmon. Recaptures as previous spawners are summarized separately since their migrations may be different from those of virgin salmon.

Tag recaptures describing the sea migrations of post-smolts and virgin salmon are from hatchery and wild smolts. All hatchery smolts were either native to the river into which they were released or of a strain from a nearby river. All tags applied to smolts were the modified Carlin type with polyethylene monofilament attachments (Saunders 1968). The previous spawner migrations are illustrated by sea recaptures of salmon tagged as 1SW and older salmon during their upstream migration and prior to spawning. These recruits were marked with several different types of dangler tags (e.g., Carlin types with polyethylene and stainless steel attachments, Floy anchor tags). All tags bore a return address. Tags recovered in the fisheries were returned voluntarily by fishermen or others associated with the fishing industry (e.g., fish plant workers) for a monetary reward. Tagging and recapture data used herein are generally a by-product of experiments conducted between the late 1960s and mid-1980s by several investigators, including myself.

2.3.1.1. Post-smolt migrations

Post-smolt recaptures are grouped under four geographic areas of population origin: upper Bay of Fundy, lower Bay of Fundy and Gulf of Maine, Atlantic coast of Nova Scotia, and Gulf of St. Lawrence. Recaptures from Maine and Quebec populations are included to facilitate comparisons and enhance the pools of post-smolt recaptures for populations in the different areas. Data for Maine and Quebec salmon were extracted from published reports (Caron 1983; Meister 1984).

Recaptures as post-smolts are summarized in Tables 1a to 1d by recovery location and month. Recaptures from populations inhabiting rivers in the same geographic areas are summarized in the same table to ease comparisons. The low incidence of post-smolt recaptures for all populations is partly attributed to their small size (i.e., <0.5 kg) and low catchability in most fishing gear. Temporal patterns in recapture data may be biased because of seasonal variation in fishing effort. Most post-smolt recaptures were in gear licensed for herring (Clupea harengus) and mackerel (Scomber scombrus).

Post-smolt recaptures of upper Bay of Fundy salmon (e.g., from Big Salmon River) were limited to the Bay of Fundy (Table 1a) whereas post-smolt recaptures from populations of the other geographic areas were distributed in coastal fisheries from the

home river to Labrador (Tables 1b to 1d). Post-smolt recaptures in the Bay of Fundy from Maine rivers and the Saint John River were returned largely from the Nova Scotia coast (90%), whereas more than half (58%) of the post-smolts from Big Salmon River were recaptured along the New Brunswick coast, west of the Saint John River.

Post-smolt recaptures from Maine and Saint John rivers suggest a migration across the Gulf of Maine and lower Bay of Fundy and northeast along the Nova Scotia coast (Table 1b). Recaptures of salmon from rivers in southwest Nova Scotia show a similar outbound migration to the south coast of Newfoundland (Table 1c). Numbers of post-smolt recaptures of these southern populations decline with distance from the home river and except for recaptures in the Bay of Fundy, most were made in June and July. Bay of Fundy recaptures accounted for 46% of all post-smolt recaptures for populations of Maine and the Saint John River. More than half of these recaptures were in August or later.

No post-smolt recaptures from populations of Maine, Saint John and southwest Nova Scotian rivers were recorded east of Area I along the Newfoundland south coast or on the east coast south of Area C. A few recaptures from these southern populations were recorded further north and two from each of the Saint John and southwest Nova Scotian populations were made in the Strait of Belle Isle area (i.e., two on the Quebec lower North Shore and two in the Area N, Newfoundland). All four recaptures in the Strait of Belle Isle area were in July and fit a sequential migration from Area J north along the west coast of Newfoundland. None of the Maine smolts were recaptured along the west coast of Newfoundland or in the area of the Strait of Belle Isle, although one was recaptured along the southern Labrador coast in July and three others in Areas B and C in August and September. The most direct migration route for the Labrador recovery is by way of the west coast of Newfoundland. The lateness of the recaptures in Areas B and C makes these recovery sites equally accessible by either the west coast of Newfoundland or a more eastern route.

Three post-smolt recaptures from rivers draining into the Gulf of St. Lawrence were recorded north as far as southern Labrador and one as far as the Bay of Fundy (Table 1d). Most post-smolt recaptures from Gulf populations were in the northern Gulf of St. Lawrence. Nine of the 20 recaptures beyond the river mouth were in areas bordering (Area N and Quebec lower North Shore) or near (southern Labrador and Area A) the Strait of Belle Isle. No recaptures were made in Areas I and J, Newfoundland, common sites for recaptures from southern non-Gulf populations (Table 1b and 1c). The anomalies in recaptures to a migration through the Strait of Belle Isle are one recapture in Area F, the southwest tip of insular Newfoundland, three along Cape Breton's

east coast and one in the Bay of Fundy. Two of the recaptures along Cape Breton's east coast originated from the Margaree River, Cape Breton. Considering the close proximity of the Margaree River to the Cabot Strait one might expect Margaree post-smolts to exit the Gulf by the Cabot Strait.

The times of recapture in the Gulf ranged from spring to fall. When recaptures in the river mouth and in and about the Strait of Belle Isle are excluded, four of the six remaining recaptures were in August and later. Three of these four recaptures originated from the Miramichi River for which only seven post-smolt recaptures were recorded outside the river mouth from more than 350,000 tagged smolts of wild and native hatchery stock origin.

2.3.1.2 Feeding and return migrations

Feeding and return migrations of four populations of salmon are illustrated by recaptures of tagged smolts as 1SW and 2SW salmon. The populations were selected because of information availability and their assumed representativeness of salmon produced in the four geographic areas under which post-smolt recaptures are summarized. The four populations are: Big Salmon River, Saint John River, upper LaHave River, and Miramichi River.

Tag recaptures were limited to 1SW and 2SW salmon since these populations produce few 3SW salmon (Ruggles and Turner 1973; Cutting and Gray 1984; Marshall 1985; Jessop 1986). Also excluded were recaptures as previous spawners. Recaptures in the river mouth were included to indicate time of return to the river and are not representative of total returns to the river.

Sea recaptures of smolts from Big Salmon accounted for 10 of 165 recoveries as 1SW and 2SW salmon. The sea recaptures were made in the Bay of Fundy except for one recovery as a 2SW salmon in Area J₂, Newfoundland (Table 2a). This lone recapture is assumed to be anomalous in the distribution of sea recaptures, including those as post-smolts (see Table 1a), which suggest that native salmon of this river confine their migrations to areas in and bordering the Bay of Fundy. Returns of 1SW and older salmon from introductions of hatchery smolts of Miramichi River origin in 1963 and 1964 (Jessop 1976) could have contributed to the 1968 smolt class which produced the lone recapture in Newfoundland. Tagged Miramichi smolts released into Big Salmon were recaptured in both Newfoundland and Greenland fisheries (Jessop 1976).

Salmon from the Saint John River first become available to directed salmon fisheries at sea age 12 months when they encounter the fishery along the south and east coasts of Newfoundland (Table 2b). Recaptures in the Newfoundland fishery

are concentrated largely in June and July and are assumed to be non-maturing salmon since recaptures along the Nova Scotia coast are few and not sequential in time to recaptures in Newfoundland. Recaptures as 1SW salmon along the Labrador coast extend from June to October. Less than 1% of the recaptures were within the Gulf of St. Lawrence. Forty-eight percent of the recaptures beyond the river mouth were made along the west coast of Greenland where they were recovered as 1SW salmon from July to November. Recaptures as 2SW salmon were not made in many areas of the sea and where present, were few considering 2SW salmon comprised more than one quarter of the recaptures in the home river.

The absence of maturing 2SW salmon of the Saint John River in fisheries beyond the river mouth indicates a return migration from northern feeding areas either prior to spring opening dates for the coastal fisheries or by an off-shore route. Small numbers of recaptures as 1SW salmon in October and November in Newfoundland Areas A, B and C and along the eastern and southwest shores of Nova Scotia may reflect the onset of a return migration in late fall for salmon destined to mature the following year. May to August 1SW salmon recaptures along the Nova Scotia coast and in the Bay of Fundy were probably maturing salmon.

Smolts released into the LaHave River were recaptured in sea fisheries as both 1SW and 2SW salmon (Table 2c). Similar to recaptures of Saint John salmon, LaHave 1SW salmon recaptures were distributed along the West Greenland coast and the east and south coasts of Newfoundland-Labrador. LaHave 1SW salmon recaptures in the Newfoundland-Labrador fishery were generally earlier and distributed more southerly than Saint John 1SW salmon recaptures. Recaptures along the Nova Scotia coast indicate a June-July migration along this coastal section for 1SW salmon returning to the LaHave River. The concentration of 2SW salmon recaptures in the river mouth in May and June and their near absence along the Nova Scotia coast suggest either an off-shore return migration of 2SW salmon or a return prior to mid-April, the opening date for the fisheries in these areas. The absence of 1SW salmon recaptures in August along the Nova Scotia coast may be attributed partially to seasonal reductions in fishing effort and gear efficiency. The 2SW salmon recaptures in Newfoundland were made largely in May and June (13 of 14 recaptures). These fish were presumably maturing since 3SW salmon are infrequent among returns to the LaHave River (Cutting and Gray 1984). The LaHave 1SW salmon recaptures in the coastal fishery of Newfoundland-Labrador were probably a mixture of maturing and non-maturing salmon since about 60% of the recoveries were in May and June and almost 70% were in southern Areas D to L.

Sea recaptures of tagged smolts from the Miramichi River as

1SW and 2SW salmon were mainly from outside the Gulf of St. Lawrence (98%) and east and north of the Cabot Strait (96%) (Table 2d). Earliest recoveries after the first year at sea were in June and made in the fishery along the south and east coasts of insular Newfoundland. Recaptures as 1SW salmon were recorded from June to August along both coasts but not in the fall fishery in Areas A, B and C. Miramichi 1SW salmon recaptures were also recorded along the west coast of Greenland from early July to late November. Recaptures as 2SW salmon in the Newfoundland-Labrador fishery almost equalled the recaptures as 1SW salmon (i.e., 185 2SW vs 244 1SW). The 2SW salmon were recaptured about one month earlier and more along the south coast than the 1SW salmon. Most of the 2SW salmon recaptures are assumed to be maturing since there are few 3SW salmon among returns to the Miramichi River (Ruggles and Turner 1973). The 1SW salmon recaptures could be a mixture of maturing and non-maturing salmon considering their temporal and spatial distributions along the Newfoundland-Labrador coasts. Maturity status of Miramichi salmon recaptured as 1SW salmon in the Newfoundland-Labrador fishery has been categorized previously on the basis of time and location of capture as 60% non-maturing (Pippy 1982). The abundance of both 1SW and 2SW salmon recaptures along the south coast of Newfoundland and the near absence of recaptures in or near the Strait of Belle Isle (3 of 707 sea recaptures) suggest that the Cabot Strait is the main return route from the northwest Atlantic for maturing salmon of the Miramichi River.

2.3.1.3 Previous spawner migrations

Descriptions of previous spawner migrations are limited by availability of tag recapture data to populations of the Saint John and Miramichi rivers (Tables 3a and 3b). It is assumed that most spawners re-entered the sea in May of year 1. Salmon recaptured during July and August of year 1 in the home river are probably consecutive-year spawners. Previous spawners recaptured far from the river mouth would have become alternate-year spawners, returning in year 2.

Recaptures of previous spawners from the Saint John show an outbound migration across the Bay of Fundy, northeast along the Nova Scotia coast to the south coast of Newfoundland, and east and north to east of Newfoundland and West Greenland (Table 3a). Several of the migrants reach the south coast of Newfoundland by late June and July and West Greenland by August in year 1. Previous spawners of the Miramichi also arrive at West Greenland by August, but by way of the Strait of Belle Isle (Table 3b). Tag recaptures at both ends of the Strait of Belle Isle are most concentrated in July, which is assumed to be the month when most previous spawners of the Miramichi exit the Gulf of St. Lawrence.

The main return route of previous spawners to the Saint John is not apparent from tag recaptures which are negligible in year 2 outside the river mouth. Recaptures of previous spawners from the Miramichi indicate that their main return migration is by way of the east and south coasts of Newfoundland. According to these data, Miramichi previous spawners mainly exit the Gulf of St. Lawrence by the Strait of Belle Isle and return by the Cabot Strait.

2.3.1.4 Comparison of return migrations of previous spawners and 2SW salmon

The similarity between return migrations to the Miramichi River of previous spawners and virgin 2SW salmon was assessed by comparing the temporal and spatial distributions of previous spawner sea recaptures in year 2 following spawning to expected distributions defined by smolt recaptures as virgin 2SW salmon. In this comparison recaptures were limited to those in the Newfoundland-Labrador fishery since they represented 94% of the sea recaptures as virgin 2SW salmon. The few recaptures outside the Newfoundland area were assumed to be incidental to main migratory patterns. Recaptures were separated into early (May and June) and late (July to September) recovery periods while spatial distributions were defined according to four geographic divisions: northeast coast (Labrador and Areas A and B), southeast coast (Areas C to F), south coast (Areas G to K), and west coast (Areas L to N).

Chi-square analyses showed neither temporal (chi-square = 0.214, $df = 1$) nor spatial distributions (chi-square 0.305, $df = 3$) of previous spawners to vary significantly ($p > 0.05$) from the distributions of virgin 2SW salmon. Because of the small number of previous spawner recaptures (29) and the possibility of misclassification of previous spawning history (e.g., a previous spawner recaptured in year 2 may have spawned in both year 0 and 1), these results should be viewed with caution. They do however suggest similarities between the return migrations of previous spawners and virgin 2SW salmon of the Miramichi. This same tendency appears common to salmon of the Saint John (see Tables 2b and 3a) and those originating from Maine (Meister 1984), except that the evidence for these southern populations is a near absence of sea recaptures in the return year of both previous spawners and virgin 2SW salmon.

2.3.2 Variation in latitudinal distribution

2.3.2.1 In Newfoundland fishery

The significance of annual variation in the latitudinal

distribution of the salmon catch along the Newfoundland coast was assessed using catches of small and large salmon (Table 4) and tag recaptures from marked smolts of the Miramichi, Saint John, and LaHave rivers (Tables 5a and 5b). The catches and recaptures in Areas A plus B were expressed as proportions of their respective totals for Areas A to I (i.e., east and south coasts except Area J). Proportions were used rather than absolute catches or recaptures to eliminate effects of variable stock strength expected because of annual variations in marine natural mortality and in number of smolts entering the sea. Tag recapture numbers were affected by the number of smolts tagged, which varied considerably.

The boundary between Areas B and C served to partition the east coast of insular Newfoundland near its mid-point. On average, about half of the catches of small and large salmon in Areas A to I were recorded in Areas A and B (i.e., the northern sector) (Table 4). A more precise breakdown of catches and recaptures by area was not attempted because all four tag recapture sets had few recaptures in some years.

Annual variation in north-south distribution was assessed by testing the proportions of catches and tag recaptures in Areas A plus B for homogeneity among years (Snedecor and Cochran 1967).

Chi-square values indicated highly significant ($p < 0.001$) variation among annual proportions in all but one of the six data series (Table 6). The exception was recorded for the 2SW salmon recaptures originating from wild smolts of the Miramichi. The chi-square value for this series approached significance ($p = 0.103$). Low numbers of recaptures in Areas A to I (i.e., 13 or less) in all but three years would have contributed to this lack of significance. The proportion of Miramichi 2SW salmon recovered in Areas A plus B ranged from 0 to 0.5 (Table 5a). These analyses suggest the presence of large annual variation in the north-south distribution of the spring-summer catches of salmon of different populations and sea ages along the east coast of Newfoundland.

2.3.2.2 In Northwest Atlantic

Annual variation in the latitudinal distribution of salmon in the northwest Atlantic was assessed using data from smolt tagging studies carried out on the Saint John River, 1969 to 1983. The assessment involved testing the linear relationship between the proportions recaptured as 1SW salmon (non-maturing) in the Newfoundland-Labrador fishery and at Greenland in the same year. Recapture proportions were assumed to represent relative abundances of tagged Saint John salmon in these two fishing areas. A negative correlation was expected if variations in

recapture proportions for these two fisheries were related to shifts in the north-south distributions of salmon in the northwest Atlantic.

To compensate for the change in fishing effort at Greenland, with introduction of the 1190 tonne quota, the recapture proportions for the Greenland fishery prior to 1976 were halved. The magnitude of this adjustment approximates the change in the catch since 1975 (i.e., the 1976 to 1984 average catch was 46% of the 1970 to 1975 average catch).

Recapture proportions were determined for 1SW salmon recovered in the Newfoundland-Labrador fishery and at Greenland by dividing the number of recaptures in each of these fisheries by the total number (n_i) of recaptures of non-maturing 1SW salmon and MSW salmon in sea fisheries and the home river (Table 7). Recaptures in the river included trap counts representative of escapements plus those returned from Indian, recreational and commercial fisheries. Recaptures outside the Newfoundland-Labrador and Greenland fisheries comprised 65 to 90% of all recoveries. The recapture proportions (p_i) for the Newfoundland-Labrador fishery were transformed to their logits, $\ln(p_i/(1-p_i))$, because the range in values of p_i was narrow and close to zero (Snedecor and Cochran 1967). The Greenland recapture proportions were both assigned ranks from 1 (lowest) to 15 (highest) and transformed to their logits. The representativeness of the ranks was tested by regressing the transformed recapture proportions for the Greenland fishery (Y) against the corresponding ranks (X) (Snedecor and Cochran 1967). A weighted regression model was used with individual weights (w_i) equal to the inverse of the estimated variances of the individual proportions, i.e., $w_i = n_i p_i (1-p_i)$ (Snedecor and Cochran 1967). This regression was highly significant ($F = 126.74$, $df = 1, 13$, $p < 0.001$), thereby confirming the representativeness of the ranks. The final step in the analysis involved regression of the transformed recapture proportions for the Newfoundland-Labrador fishery (Y) against the rank of the Greenland recapture proportion (X).

The regression was negative ($F = 12.79$, $df = 1, 13$, $p = 0.003$), indicating a low abundance of non-maturing 1SW salmon in one area when numerous in the other. This result suggests that Saint John salmon caught in Newfoundland-Labrador and Greenland fisheries, separated by more than 1000 km of sea and one to two months migration time, are of a common migratory group that overwinters near insular Newfoundland.

2.3.3 Temperature effects on distribution

2.3.3.1 In Newfoundland fishery

The proportions of catches and tag recaptures taken in Newfoundland Areas A plus B (Tables 4, 5a and 5b) were regressed against an index of prevailing SST in spring. The temperature index, reflecting the time of spring warm-up, is the Julian day on which the 0°C isotherm in coastal waters off eastern Newfoundland receded north of 50°N (Table 8). The Julian day measurements were determined from SST charts of the Canadian Forces Meteorological and Oceanographic Centre (METOC), Atmospheric Environmental Service, Department of the Environment, Canada. The charts show isotherms at 2°C intervals for the northwest Atlantic. The isotherm plots were based on data derived principally from radio weather messages and logbook records transmitted by merchant vessels. Individual charts summarized data by intervals of three to seven days. The Julian day on which the 0°C isotherm receded north of 50°N was taken as the median date of the first time interval in which this was recorded.

A weighted linear regression model similar to that described in section 2.3.2.2 was used to assess the relationship between salmon distribution and this index of SST. The independent variable ranged from day 120 (April 30) to day 187 (July 6).

All regressions were negative (Table 9), thereby indicating salmon catches and recaptures to be distributed further north along the Newfoundland coast in years when the sea warms-up early. This tendency was common to salmon of different sea ages and originating from different rivers, indicating that SST does influence the distribution of the salmon harvest along the Newfoundland coast.

2.3.3.2 In Northwest Atlantic

Greenland and Newfoundland tag recapture proportions derived for the Saint John River smolt releases (Table 7) were regressed against five indices of SST for the northwest Atlantic. These comparisons were aimed at investigating possible effects of varying SST on the exploitation of salmon from this river population in the Newfoundland-Labrador and Greenland fisheries. The temperature variables were: i) the latitude ($^{\circ}\text{N}$) of the northward extent in January of the 4°C isotherm west of 45°W (VAR1); ii) same as i except measurements were for August (VAR2); iii) the area ($\text{km}^2 \times 1000$) covered by 4°C or warmer water in January north of 50°N and west of 40°W (VAR3); iv) the extent ($\%$) of the sea along the West Greenland coast covered by the 4°C

isotherm in August north of 60°N (VAR4); and v) the Julian day on which the 0°C isotherm receded north of 50°N along the Newfoundland east coast (VAR5). Measurements for VAR1 to VAR4 were taken from Reddin and Shearer (1987) and are shown in Table 10. These were determined from monthly ice charts of the British Meteorological Office, Bracknell, England. VAR1 and VAR2 were selected because analyses by Reddin and Shearer (1987) indicated salmon abundance at Greenland to be related to these indices of sea temperature. VAR3 and VAR4 were also investigated since they are alternate measurements of the same sea temperature conditions as VAR1 and VAR2, respectively. VAR1 and VAR3 were highly correlated (i.e., $r = 0.904$, $df = 13$, $p < 0.001$) whereas the correlation between VAR2 and VAR4 was marginal (i.e., $r = 0.570$, $df = 13$, $p = 0.026$). VAR5 is given in Table 8.

A weighted linear regression model, similar to that used in section 2.3.2.2, was used to determine possible relationships between the recapture proportions for both Newfoundland and Greenland and the five SST variables.

The tag recapture proportion for Greenland was related to both VAR1 ($F = 3.624$, $df = 1,13$, $p = 0.080$) and VAR3 ($F = 6.629$, $df = 1,13$, $p = 0.023$). These relationships indicate that proportionately more Saint John River salmon were exploited at Greenland following winters in which warm sea temperatures prevailed far north in the Labrador Sea.

The Newfoundland tag recapture proportion was not significantly ($p > 0.10$) related to any of the five variables. The analysis involving VAR3 was suggestive of a relationship with a negative slope (i.e., $F = 0.823$, $df = 1,13$, $p = 0.353$), as would be expected considering the inverse relationship between recapture proportions for the Newfoundland and Greenland fisheries (refer to section 2.3.2.2) and the positive relationship between the Greenland recapture proportion and VAR3.

No relationship was apparent between VAR5 and the tag recapture proportion for either Greenland or Newfoundland fishery. VAR5 was not correlated ($p > 0.10$) with either VAR1 or VAR3, thereby indicating the independence of spring warm-up time along the Newfoundland east coast from previous winter temperature conditions in the Labrador Sea.

2.4 DISCUSSION

Post-smolt migrations of salmon populations investigated herein are difficult to interpret because recaptures were few and their representativeness of post-smolt distribution is questionable. A major gap in our knowledge of the sea distribution of salmon is their whereabouts as post-smolts.

Fifty-eight percent of all post-smolt recaptures from tagged smolts of Big Salmon River were made in the western Bay of Fundy. This western area appears to be off the migration route of salmon destined for the northwest Atlantic, i.e., according to post-smolt recaptures for salmon of Maine and the Saint John River. The western Bay of Fundy and the northern Gulf of Maine are probably the main overwintering areas for post-smolts from Big Salmon and of other upper Bay of Fundy populations showing similar life history characteristics (Amiro and McNeill 1986). Post-smolts recaptures of Big Salmon origin in the western part of the Bay during late summer support this suggestion as does the presence of suitable overwintering temperatures for salmon in the area. This latter condition is confirmed by the recent proliferation and success of salmon cage culture operations in the western Bay of Fundy.

A diffuseness in the outbound migrations of salmon from Maine and the Saint John River is indicated by their recaptures as post-smolts from June to September in the Bay of Fundy and over the same time interval along the Atlantic coast of Nova Scotia and in Areas I and J, Newfoundland. A similar ragged pattern is apparent in the post-smolt recapture data for salmon originating from and caught within the Gulf of St. Lawrence. These data indicate a broad dispersal of the post-smolts from an individual river during their outbound migration. The absence or small numbers of recaptures as post-smolts far from the river mouth probably reflect a dispersal of most post-smolts away from the coast.

The nine post-smolt recaptures in the area of the Strait of Belle Isle from rivers draining into the Gulf of St. Lawrence are insufficient to conclude that this northern passage is a major exit for post-smolts from Gulf rivers. According to tagging studies reported herein, the Strait of Belle Isle is the main exit for previous spawners of the Miramichi River. However there is not sufficient evidence to conclude that post-smolts and previous spawners follow the same outbound migration routes.

The extended period over which post-smolts from Gulf rivers were recovered within the Gulf (i.e., May through October) suggests a late departure from within the Gulf for some post-smolts. Reports of large numbers of post-smolts observed in fall along the north shore of Quebec (J.D. Dutil, Department of Fisheries and Oceans, Quebec City, Quebec, pers. comm.) support this suggestion.

Recapture data reported herein and by others (Ritter 1972; Pratt et al. 1974; Turner 1975b; Marshall 1982; Pippy 1982; Meister 1984) suggest that the migrations of most North American salmon after their first winter in the sea are from east of Newfoundland and Labrador where 1SW and older salmon are reported

to be abundant in early spring (Templeman 1967, 1968; May 1973; Reddin and Burfitt 1984). The main directions of migrations in spring and summer are west for maturing salmon and west and north for non-maturing salmon. An initial westward migration by non-maturing 1SW salmon is indicated by their presence in catches along the Newfoundland and Labrador coasts (Idler et al. 1981) and tag recaptures for salmon of the Saint John River. The inverse relationship between tag recapture proportions for Saint John River salmon in the Newfoundland-Labrador fishery and at Greenland suggests that these main fishing areas are points along a common northward migration route for non-maturing 1SW salmon. Salmon migrating along the east coast of Newfoundland in spring could be available to the fishery at Greenland one to two months later assuming an average migration speed of 32 km/day (Pippy 1982). Considering that salmon are generally available at Greenland from mid-July to late fall (Christensen and Lear 1980), it is probable that the main migration from the Newfoundland area to Greenland occurs during late spring and early summer.

The time of return migrations from east of Newfoundland is variable among populations from the different areas. Main migrations of salmon returning to the Saint John River are assumed to occur from late fall to early spring and possibly offshore since almost no tag recaptures as 2SW salmon are recorded beyond the river mouth and only a few are reported as 1SW salmon between Newfoundland and the Bay of Fundy. A return during late fall is indicated by recaptures in October and November along the northeast coast of Newfoundland and the Atlantic coast of Nova Scotia. Meister (1984) reported similar migration patterns for salmon of Maine rivers. A return to southern rivers during late fall of the year prior to spawning is also supported by anecdotal reports of immature salmon recruits along the Nova Scotia coast in November (Hardy 1869).

Salmon returning to the LaHave and Miramichi rivers leave the Newfoundland area later than salmon returning to rivers further south since maturing salmon of both these populations are recaptured along the Newfoundland east and south coasts in spring and early summer. LaHave salmon are also recaptured in coastal fisheries between Newfoundland and their home river. According to these and other marking study results (Murray 1968; Ritter 1972; Tetreault and Carter 1972; Turner 1975b; Marshall 1982; Pippy 1982), the return migrations to the LaHave and Miramichi rivers from east of Newfoundland typify those of most other populations.

Salmon returning to the Miramichi from east of Newfoundland use the Cabot Strait route according to recaptures from both smolt and previous spawner tagging studies. Results of other smolt tagging studies confirm use of this southern route by salmon returning to rivers emptying into the southern and western

Gulf of St. Lawrence (Ritter 1972; Tetreault and Carter 1972; Pippy 1982). According to marine tagging studies the Strait of Belle Isle route is used only by salmon returning to the eastern part of the north shore of Quebec and the northern part of the west coast of Newfoundland (Belding 1940).

The distribution of tag recaptures of all sea ages in the sea fisheries confirm the presence of two different marine feeding areas for North American Atlantic salmon. Salmon of Big Salmon River, and probably other upper Bay of Fundy populations of the same life history type, e.g., Stewiacke River population (Amiro and McNeill 1986), limit their migrations to the Bay of Fundy and perhaps its western bordering areas. Other populations of salmon, as indicated by recapture data reported herein and by others (Murray 1968; Ritter 1972; Tetreault and Carter 1972; Pratt et al. 1974; Turner 1975a; 1975b; Lear and Day 1977; Marshall 1982; Meister 1984), migrate to and from the northwest Atlantic east of Newfoundland. This northern feeding area, which extends from the southern Grand Bank (43°N) (Lear 1976; Reddin and Burfitt 1984) to Disko Bay, Greenland (70°N) (Templeman 1967, 1968; May 1973; Christensen and Lear 1980), appears to be the common feeding area for all North American salmon populations except those of the upper Bay of Fundy.

The return migration of previous spawners from the Miramichi River showed significant similarities in timing and route to those of virgin 2SW salmon. Although a similar comparison between return migrations of previous spawners and virgin 1SW salmon of the Miramichi was not attempted, because of the difficulty in differentiating between maturing and non-maturing 1SW salmon recaptures in the Newfoundland fishery, their return migrations are not expected to be similar. Return migrations of 1SW salmon are generally later than those of 2SW salmon, as apparent from recaptures of tagged Miramichi salmon of both sea ages along the south coast of Newfoundland (Table 2d). Similarly, 1SW salmon enroute to the LaHave River are caught later along the coasts of both southern Newfoundland and Nova Scotia than 2SW salmon homing to the LaHave (Table 2c). The return migrations of maturing 1SW salmon and previous spawners might also differ because these two sea-age groups are probably returning from different areas of the sea. Many of the Miramichi and Saint John previous spawners (Table 3a and 3b) and virgin 2SW salmon (Table 2b and 2d) would have spent their previous summer and fall in the Davis Strait whereas maturing 1SW salmon of these same populations would not probably have migrated as far north in their post-smolt year.

The observations that proportionately more salmon are caught further north along the east coast of Newfoundland in years in which warm local sea temperatures prevail early in spring are interpreted as reflecting shifts in salmon distribution rather

than changes in fishing effort or gear efficiency. This interpretation is supported by Reddin and Shearer (1987) who noted that the extreme southern distribution of the 2SW salmon recaptures from one of three tagged smolt classes of the Sand Hill River coincided with colder than normal spring temperature conditions along the Newfoundland coast. This shift in distribution suggests an avoidance of cold sea temperatures by Sand Hill salmon homing to their northern river. This avoidance of cold sea temperatures is also apparent in the catch rates for experimental drift net sets in the northwest Atlantic (May 1973; Christensen and Lear 1980; Reddin and Shearer 1987).

The consistency of the relationship between salmon distribution and sea temperature along the Newfoundland coast for salmon of different sea ages is not supported by the observation reported by Reddin and Shearer (1987). They noted no variation in the distribution of tagged 1SW salmon homing to the Sand Hill River despite variation in local sea temperatures which affected the distribution of the population's 2SW salmon. This discrepancy is presumed to reflect the limited data base (i.e., three years of recaptures) examined by Reddin and Shearer (1987).

The evidence that 1SW salmon of the Saint John are more abundant at Greenland following a winter during which warm sea temperatures prevailed far north in the Labrador Sea is consistent with results reported by Reddin and Shearer (1987). They showed that salmon in general, were more abundant at Greenland following a warm winter in the Labrador Sea.

Although the latitudinal distribution of the salmon catch along the Newfoundland coast varied with local sea temperature in spring, the rate at which salmon of the Saint John were exploited in the Newfoundland fishery seems independent of this same variable. This inconsistency and the observed independence of spring sea temperatures along the Newfoundland coast and prior winter conditions in the Labrador Sea suggest that a hierarchical system of sea temperature conditions influences the salmon harvest in the Newfoundland-Labrador fishery. It is proposed that conditions in the Labrador Sea during the winter affect the distribution of salmon between Greenland and Newfoundland and hence their potential availability to the fisheries in these two areas. Subsequently, the distribution of salmon in the Newfoundland area is affected by coastal sea temperatures in early spring.

Failure of analyses involving Saint John tag recaptures to implicate August temperature conditions in the Davis Strait (i.e., either VAR2 or VAR4) as affecting the recapture proportion for Greenland is inconsistent with results reported by Reddin and Shearer (1987). Their analyses linked the availability of salmon at Greenland to VAR2. They suggested that August temperature

conditions in the Davis Strait affected movement of salmon into the fishing area at Greenland. The discrepancy between results of these two analyses reflects the preliminary nature of both and thereby emphasizes the importance of further investigation of the potential effects of varying environmental conditions on the distribution and harvest of salmon in the northwest Atlantic.

2.5 CONCLUSIONS

Investigations reported herein confirm existence of two main feeding areas for North American Atlantic salmon; upper Bay of Fundy populations limit their migrations to the Bay of Fundy area while other populations migrate to and from the northwest Atlantic east of Newfoundland. Migrations of salmon feeding in the northwest Atlantic vary temporally and spatially with river of origin and as a result, populations are differentially vulnerable to the sea fisheries and probably experience different natural mortality rates.

Analyses indicate that sea temperature conditions influence marine distribution and fishing mortality. Annual variation in sea temperatures may therefore be expected to affect returns to home rivers, except possibly upper Bay of Fundy rivers, to which returns would be unaffected unless rate of natural mortality was also influenced.

3.0 MARINE NATURAL MORTALITY

3.1 INTRODUCTION

Salmon experience mortality in the sea from both fishing and natural causes. Fishing mortality may be subdivided into catch and non-catch losses, the latter attributed to fishing but not included in catch statistics (Ricker 1976). The combined effects of marine fisheries and natural mortality reduce returns of 1SW and older salmon to the river to 15% or less of the number of smolts that previously entered the sea (Elson 1957; Bergeron 1959; Murray 1968; Pratt et al. 1974; Chadwick and Meerburg 1978; Jessop 1986). Partitioning of this mortality between losses attributed to fishing and natural causes is often not possible because marking data are either unavailable or inadequate to estimate fisheries effects. Estimates of fishing mortality derived from marking data are potentially biased if recaptures are incorrectly adjusted for non-reported recoveries and non-catch fishing mortality (Anon. 1985a). Similarly, estimates of survival or mortality would be biased if they were incorrectly adjusted for handicap effects attributed to the marking and counting of smolts (Jessop 1975, 1986; Ricker 1975).

This section provides estimates of marine natural mortality experienced as post-smolts and between spawnings, and presents analyses aimed at identifying factors associated with or potentially contributing to variation in marine natural mortality.

3.2 LITERATURE REVIEW

The component of marine mortality attributed to natural causes exceeds the losses caused by fishing. Recent estimates indicate smolt survival to Baltic Sea fisheries and spawning escapements to vary between 5 and 48% for hatchery smolts and 34 and 51% for wild smolts (Anon. 1983). For wild smolts of the Bush River, Northern Ireland, Doubleday et al. (1979) estimated smolt survival to be about 15%. Shearer (1984) reported estimates for smolts of the North Esk River, Scotland, which averaged about twice that determined for Bush River salmon. For Icelandic salmon, Ísaksson et al. (1978) estimated survival of wild smolts of the Ellidaar River to be about 26%. This estimate, derived for one smolt class, pertains to a population that produces only 1SW salmon (Ísaksson et al. 1978) and is not exploited by sea fisheries (Ísaksson 1980).

Estimates of smolt-to-recruit survival for North American salmon are few and generally unreliable because of data inadequacies and flaws in the methodology by which they were derived. Doubleday et al. (1979), using enumeration and smolt tag recapture data for three smolt classes of salmon of the Sand Hill River (Pratt et al. 1974), estimated smolt survival to the 1SW salmon stage to be 18%. Contributions to the sea fisheries were estimated from tag recaptures and ratios of tagged:untagged salmon recovered in the river. The survival rate determined by this method is negatively biased because underlying the ratios used is the assumption that tagged and untagged smolts survive equally. The observed 1:11 ratio of return rates for tagged and untagged smolts seems largely attributable to differential mortality rather than tag loss as assumed by Doubleday et al. (1979). Ísaksson and Bergman (1978) reported an average tag loss rate of 10% for hatchery smolts marked with the same type of tag, i.e., Carlin tags (Saunders 1968). The estimate of survival for the Sand Hill smolts is further negatively biased because no adjustments were made for non-catch fishing mortality or incomplete reporting of tags recovered in the sea fisheries.

Jessop (1986) estimated the return of 1SW salmon from unmarked smolts of Big Salmon River to average 4.5%. This estimate does not represent total survival to fisheries and the spawning escapement since it fails to include MSW salmon returns, reported by Jessop (1986) to account for about 7% of the total return of virgin fish, and the exploitation in sea fisheries, determined from tagging studies to be about 7% of the total

recaptures (Jessop 1976). This estimate is further negatively biased because of handling effects attributed to trapping and counting the smolts and for which a known mortality of 2.3 to 10.1% was recorded (Jessop 1975). The magnitude of this latter bias is unknown since the reported losses do not account for the delayed mortalities caused by handling.

A third estimate of smolt-to-recruit survival for North American salmon was reported by Chadwick et al. (1985) for the 1SW salmon population of Western Arm Brook, Newfoundland. The estimate was based on the 1976 smolt count and the 1977 1SW salmon return to the river. Sea fisheries contributions were estimated from a marine tagging study carried-out locally in 1977 and tag recaptures from a five-year tagging study involving previous spawners. Survival of the 1976 smolts to the 1SW salmon stage was estimated to be 16.5%. Distant and local sea fisheries accounted for 65% of the survivors. The authors concluded that this estimate of survival was a minimum value considering that the 1978 smolt class yielded a 12% return of 1SW salmon to the river (i.e., the return after sea fisheries).

Estimates of the survival of previous spawners re-entering the sea are not available, although they are presumed to be low for most populations considering the low incidence of previous spawners in both fisheries catches and river escapements. For instance, the average incidence in a sample of 9866 fish caught at Greenland from 1965 to 1972 was 1.2% (Munro and Swain 1980). In a pooled sample of 3392 fish collected from the Newfoundland-Labrador commercial fishery in 1969 and 1970, the incidence of previous spawners among large salmon averaged 5.7% (Lear and May 1972). This fishery harvests about 0.5 million fish annually of which 57% in these years were small salmon (Anon. 1985a). Relative to the total catch of salmon in this fishery the incidence of previous spawners was about 2.5%. Within escapements to North American rivers the incidence of previous spawners is generally lower than 10% and often less than 5% (Schaffer and Elson 1975). An exception to this tendency is apparent in aging data for salmon returning to Big Salmon River, among which previous spawners averaged close to 50% of the return to the river from 1964 to 1973 (Jessop 1986). Salmon of Big Salmon mature first mainly as 1SW salmon (93%) and spawn in consecutive rather than alternate years (Jessop 1986). Ducharme (1969) reported salmon of this river returning for their fifth and sixth consecutive spawning trips. Similar patterns in repeat spawning are apparent in salmon populations of other upper Bay of Fundy rivers, e.g., Stewiacke River (Amiro and McNeill 1986).

The natural mortality rate for salmon in the sea varies both annually and among populations (Reddin and Carscadden 1982; Porter and Ritter 1984; Scarnecchia 1984a, 1984b). The low

abundance of recruits from the 1977 smolt class in 1978 and 1979 Canadian catches illustrates annual variability. The yield of the 1977 smolt class to Canadian fisheries was 1025 tonnes or 50% of the mean for smolt classes 1969 to 1982 (Anon. 1985b). This low abundance, also manifested in spawning escapements of several North American rivers (Marshall 1985; Chadwick and Peppar 1985; Cutting and Jefferson 1985; Randall et al. 1985a, 1986), could not be attributed to low smolt production in 1977 (Reddin and Carscadden 1982). The 1982 and 1983 smolt classes of many North American populations also experienced above average marine natural mortality (Anon. 1984, 1985b; Porter and Ritter 1984).

Natural mortality experienced by Atlantic and Pacific (*Oncorhynchus* spp.) salmon is high during the early sea life and low in the final months or years spent in the sea (Carlin 1962; Larsson 1975; Mathews and Buckley 1976; Ricker 1976; Doubleday et al. 1979). Ricker (1976), in a review of methods used to estimate natural mortality, reported a range in mean monthly instantaneous rates for sockeye salmon (*O. nerka*) in their penultimate sea-year of between 0.012 and 0.019 (corresponding annual survival rates are 87 and 80%). He also reported similar rates for coho (*O. kisutch*) and chum (*C. keta*) salmon. Atlantic salmon smolts entering the Baltic Sea were estimated by both Carlin (1962) and Larsson (1975) to be reduced to about 15% of their original abundance in the first sea-year because of natural mortality. Their estimates were based on tag recaptures for hatchery smolts and an assumed annual natural mortality rate of 0.1 after the first sea-year. Assumption of higher mortality rates after the first sea-year (i.e., 0.2 and 0.3) by Carlin (1962) yielded less realistic estimates of mortality attributed to both fishing and natural causes (Christensen and Johansson 1975; Larsson 1975). An annual rate of 0.1 for Baltic salmon after the first sea-year is in broad agreement with rates assumed by the ICES Working Group on North Atlantic Salmon for salmon stocks in the north Atlantic (Anon. 1981, 1984). The Working Group, in its assessment of impact on homewater stocks of the Greenland, Faroese and Norwegian Sea fisheries, assumed monthly natural mortality rates of 0.006 to 0.016, for salmon approaching or older than one sea-year.

Natural mortality rates assumed by the ICES Working Group were based on estimates by Doubleday et al. (1979) for salmon of the Bush (Northern Ireland) and Sand Hill (Canada) rivers. The estimates were determined by the inverse weight method, originally proposed by Mathews and Buckley (1976) to estimate rates of natural mortality in the sea for coho salmon. The method assumes that rate of natural mortality varies inversely with weight-at-age, premised on the assumption that natural mortality is due primarily to predation (Cushing 1974). Ricker (1976) concluded that the inverse weight method provides reasonable estimates for Pacific salmon given their similarity to

rates derived by other methods. Doubleday et al. (1979) provided support for the validity of the inverse weight method by testing the relationship with return rate data for Atlantic salmon wild smolts of different sizes from the Bush River. The hypothesis is supported also by sea survival estimates for wild smolts emigrating from the Little Codroy River. In this instance, the older and larger wild smolts yielded higher recapture rates (Murray 1968). Anomalous to this tendency is the report by Chadwick et al. (1978) that sea survival of wild smolts from Western Arm Brook displays no consistent pattern with smolt size. An explanation for this anomaly possibly lies with the size selective nature of the sea fisheries. For instance, Chadwick (1982) reported a difference of more than 1 cm in the mean lengths of 1SW salmon taken in the local commercial fishery (i.e., in St. Barb Bay) and at the counting fence on Western Arm Brook. The primary gear type in this fishery and others nearby, through which Western Arm Brook fish may pass on their return migration, is the fixed gill net which is selective for the larger 1SW salmon.

A direct relationship between marine survival and juvenile or smolt size is evident for both wild (Ward and Slaney 1988) and hatchery (Wagner 1967; Wallis 1976) steelhead trout (*O. mykiss*), and hatchery chinook salmon (*O. tshawytscha*) (Reisenbichler et al. 1982; Bilton 1984), coho salmon (Johnson 1970; Hager and Noble 1976) and Atlantic salmon (Carlin 1968; Ísaksson 1976a; Larsson 1977b; Ritter 1977). The relationships for Atlantic salmon were based on tagging studies in which Carlin-type tags (Saunders 1968) were used. According to Icelandic studies, in which hatchery smolts were marked with magnetic wire nose tags (Jefferts et al. 1963), these relationships are in part an artifact of higher tag loss and tagging mortality among the smaller smolts (Ísaksson and Bergman 1978).

The linearity of the relationship between sea survival and fork length of hatchery smolts disappears at 19 to 22 cm, beyond which survival either levels off or decreases (Carlin 1968; Ísaksson 1976a; Larsson 1977b; Ritter 1977). This tendency may be attributed to a "desmoltification" of the larger individuals (Anon. 1983). These larger smolts might have greater difficulty in adapting to salt water and thereby experience greater predation (Bakshtansky et al. 1979, 1980; Anon 1983).

Circumstantial evidence is strong that marine natural mortality of salmon largely results from predation (Cushing 1974) and that the rate varies with fish size, particularly during the early weeks or months of sea life (Mathews and Buckley 1976; Ricker 1976). The rate of natural mortality after the first year at sea is probably constant and relatively low (i.e., mean monthly instantaneous rate <0.02), since the animal is less vulnerable to predation and losses to senescence (Comfort 1979)

should be negligible considering that fish are potentially capable of reproducing.

The list of predators of Atlantic salmon is long although information on their effect on survival of salmon in the sea is sketchy. Much of the literature pertains to predation of smolts during their migration downstream and through the estuary (Piggins 1958; Meister 1969; Larsson 1985; Hvidsten and Møkkelgjerd 1987). Most of these reports of predation on salmon are isolated incidences and might not represent the common situation.

Avian predation of salmon in the sea would be largely confined to the early post-smolt stage. By the end of the first summer in the sea, post-smolts exceed 250 g (Allen et al. 1972) and presumably are beyond the prey size limit of most avian predators (Ricker 1976; Shearer 1984). Avian predators probably include most fish foraging seabirds that are large enough to consume a post-smolt. Species of birds that prey upon smolts in the river might also do so in the estuary and along the open coast. Common representatives of this category are mergansers (Mergus spp.), cormorants (Phalacrocorax spp.) and gulls (Larus spp.) (Anon. 1983). Other seabirds that are large enough to prey on post-smolts and are found along the North American coast include the northern gannet (Sula bassanus), shearwaters (Puffinus spp.), the common murre (Uria aalge) and the northern fulmar (Fulmarus fulmarus). A recent report of ten salmon tags found on Funk Island, Area B, Newfoundland, confirm predation of post-smolts by large sea birds in coastal waters more than 1000 km from the salmon's home river (Montevecchi et al. 1988). These tags were from smolts released in Maine, southern New Brunswick and southern Nova Scotia. Five of the tags were in regurgitations of northern gannets. As well, the authors reported the recovery of a tag that had been applied to a smolt released in the St. Croix River (i.e., on the Maine-New Brunswick border), from a common murre at Witless Bay, Area F, Newfoundland.

Fish species which prey on salmon are potentially numerous (Anon. 1983). Larsson (1985) reported heavy predation of both wild and hatchery smolts by burbot (Lota lota) and pike (Esox lucius) in Swedish rivers. He estimated that a burbot population, in the area where smolts have been released annually into the River Lule, consumed at least 26% of the 662,000 smolts liberated that year. He suggested that burbot congregated at the release site with the first smolt releases. Similarly, Piggins (1958) suggested that pollack (Gadus pollachius) and coalfish (G. virens) congregate in the estuary of the Burrishoole River, Southern Ireland, during the smolt run. In Norway, studies in the estuaries of the River Surna and River Orkla defined cod (G. morhua) predation rates at 24.8 and 20.0%, respectively (Hvidsten

and Møkkelgjerd 1987; Gunnerød et al. 1988). Larsson (1980) reported finding post-smolts in cod collected off a Swedish west coast river. Among tag recaptures for Swedish smolts, 7 of 1810 recorded for predators since 1969 were found in cod (Anon 1983). One of the Swedish tags assigned to predators was recovered from the stomach of a salmon. In North America, the known fish predators of smolts included only chain pickerel (Esox niger) (Meister 1969) and sea trout (Salvelinus fontinalis) (Murray 1968). Predation of post-smolts in both the estuary and the sea by large carnivorous fish is suspected but not documented.

Remains of salmon were found in stomachs of sharks taken incidentally at Greenland (Templeman 1967). Although the species of shark was not always identified, salmon remains were found in the stomachs of the Greenland shark (Somniosus microcephalus) and the porbeagle (Lamna nasus). Ten salmon, ranging from 4.5 to 5.4 kg, were found in the stomach of one shark measuring 7.6 m. The severity of predation by sharks cannot be assessed from these reports since there is no indication of predation frequency or predator abundance.

The sea lamprey (Petromyzon marinus), a potential parasite of salmon, might also be causing mortality among salmon while they are in the sea. Beamish (1980) reported lamprey scar rates on adult salmon returning to the Saint John River, New Brunswick, that ranged from 2.6 to 15.0% in years 1972 to 1975. According to reports pertaining to lamprey effects on salmonid populations in the North American Great Lakes (Pycha 1980; Swanson and Swedberg 1980), the sea lamprey could be killing salmon larger than a post-smolt.

Marine mammals are also known predators of salmon in the sea. Rae (1968) reported that salmonids are an important food item of the grey seal (Halichoerus grypus) and to a lesser extent the harbour seal (Phoca vitulina) in the British Isles. Similarly, Soderberg (1975) reported salmon remains present in the stomachs of 9.6% of the grey seals and 7.7% of the ringed seals (Pusa hispida) in the Baltic Sea. He noted the size of the salmon consumed by the seals as generally ranging from 1.0 to 2.5 kg. No salmon were present in stomachs of harbour seals (Soderberg 1975) and porpoises (Phocaena phocaena) (Lindroth 1962) from the Baltic Sea.

Evidence of predation by mammals on salmon along the North American coast and at Greenland is lacking except for the incidental occurrence of salmon amongst stomach contents of grey seals (Mansfield and Beck 1977). Otters (Lutra canadensis) and harbour seals, which remove salmon from Canadian fishermen's nets (Ritter et al. 1979b; Reddin 1980), also probably prey on free swimming salmon. It is unlikely that the larger marine mammals, such as whales, impact severely on an individual salmon

population since they generally forage away from the mouths of the salmon producing rivers and are non-discriminatory in their feeding habits (Katona et al. 1983).

Predation of salmon in the marine environment would be greatest during the early phase of the salmon's migration. With time at sea, the salmon grows beyond the size range of its predators. For example, Atlantic cod prefer potential prey fish which are about one tenth their own body weight (Ursin 1973; Anderson and Ursin 1977). The estuary and coastal waters which salmon pass through first are probably the areas of heaviest predator concentration. Piscivorous fish likely account for most of the predation loss. This suggestion is supported by estimates of the disposition of capelin consumed by natural predators. Brown and Nettleship (1984) estimated that the amount of capelin (Mallotus villosus) consumed by Atlantic cod in Newfoundland waters is about 10 X that eaten by either seabirds or seals and whales.

Salmon food items in the northwest Atlantic are diverse, varying with the individual and its body size, and according to season and location in the sea (Templeman 1967, 1968; Lear 1980). Capelin is the main food-item for salmon along the west coast of Greenland in fall (59% of total food by weight) and during May-July along the Newfoundland-Labrador coast (40 to 99%) (Lear 1980). Other main food items in salmon off Greenland include launce (Ammodytes lanceolatus), amphipods (Amphipoda) and euphausiids (Euphausiacea). Salmon in the Davis Strait, Labrador Sea and off the northeast Newfoundland shelf feed mainly on Paralepis coregonoides borealis, Arctic squid (Gonatus fabricii), amphipods and lantern fishes (Myctophidae) (Lear 1980). Amphipods dominate the diet of the smaller salmon in the Labrador Sea in May (i.e., salmon 40-59 cm in length). This change in food items with fish size probably reflects the size limitation on prey that the smaller salmon are able to consume. The variety of food items both available and consumed by salmon in northwest Atlantic indicate opportunity for salmon to shift to other food items in times of shortage of an otherwise common food.

The sea survival of a smolt class may vary because of variation in food availability during the initial days or weeks the salmon spends in the estuary and sea. Studies on Atlantic salmon hatchery juveniles indicate rapid utilization of stored energy reserves during parr-smolt transformation (Farmer et al. 1978). Similarly, Burrows (1969) recorded a rapid depletion in lipid content in hatchery juvenile chinook salmon between release into the river and recovery in the estuary seven days later. These elevated rates in metabolism may continue through the period of adaption to seawater, a stressful time for salmon (Bakshtansky et al. 1979, 1980). A scarcity of food at this critical time could increase sea mortality. A low abundance of a

common forage consumed by older salmon would have less and perhaps no direct effect on their survival considering the presence of alternate forage species throughout the northwest Atlantic.

Sea temperature probably affects the survival of post-smolts and salmon of older sea-ages. Scarnecchia (1984a), in an assessment of environmental effects on yields of Icelandic Atlantic salmon, found recreational catches to be positively correlated with marine surface temperature in the post-smolt year for northern coastal rivers but less so for southern coastal rivers. He noted that sea temperature extremes and variation were greater off the north coast. Relationships between sea temperature and marine survival have been demonstrated also for pink salmon (*O. gorbuscha*) of the Fraser River (Vernon 1958) and chinook salmon of the Columbia River (Van Hyning 1973).

The lower lethal temperature for Atlantic salmon is -0.7°C in seawater of 30‰ salinity (Saunders et al. 1975). Salmon and other marine fishes can live for some time in temperatures lower than -0.7°C provided they do not come in contact with ice (Scholander et al. 1957). Long-term exposure of Atlantic salmon to low sea temperatures (i.e., about 1°C) may result in an osmotic imbalance (Bryne et al. 1972). The ultimate upper lethal limit, only determined for salmon in fresh water, is 27.8°C (Garside 1973).

Salmon of Ungava Bay rivers exemplify an irregular migratory behaviour because severe ice conditions and cold temperatures block their passage into and from the river estuaries (Power 1981). In some years sea-bound salmon do not leave the estuary until late summer and in extreme years they possibly remain in the estuary or return to fresh water without having gone to sea (Power 1981; Robitaille et al. 1984a, 1984b). These salmon, situated at the northern fringe of the species' natural range on the North American continent, have a relatively high risk of encounter with low lethal sea temperatures.

Surface seawaters of low lethal temperatures prevail inshore during late winter over most of the geographic range of the North American Atlantic salmon (Sutterlin et al. 1981; Saunders 1986). Warmer temperatures during winter are increasingly more prevalent south of latitude 44°N in bays or inlets protected from continuous exchange with the open sea (Saunders 1986). Warmer water also exists off-shore with SST greater than 2°C during winter extending far north and west in the Labrador Sea (Reddin and Murray 1985). Although no temperature selection studies have been done on post-smolts, there is much evidence that salmon avoid extreme low temperatures. For instance, salmon in the Davis Strait and Labrador Sea are seldom found at temperatures below 2°C (May 1973; Christensen and Lear 1980; Reddin and

Shearer 1987), salmon distribution along the Newfoundland coast varies with local sea temperatures in spring (see section 2.0) and extreme low catches of salmon at Greenland in 1983 and 1984 seem linked to abnormally cold sea temperatures (Anon. 1985b; Reddin and Murray 1985; Rosenørn et al. 1985). No evidence exists of free-ranging Atlantic salmon dying because of low sea temperatures.

Mortality attributed to extreme warm sea temperatures is unlikely since the migrations of the most southerly North American populations are northward to the Labrador Sea and Davis Strait (Meister 1984) where they remain during summer and fall. Some salmon pass through warmer seas on their return migrations, but temperatures would not approach the upper lethal limit except perhaps in southern estuaries.

A relationship between rate of natural mortality and environmental temperature is suggested by Pauly (1979). His analysis, involving 175 stocks from 84 fish species scattered from polar to tropical waters, indicates that natural mortality during the adult life span is lower in stocks that inhabit colder waters. Several hypotheses for this relationship were offered, ranging from greater physiological mortality due to disease or old age to higher predation because of greater metabolic needs at warmer temperatures. Although Pauly (1979) excluded data for Pacific and Atlantic salmon, because of the requirement that natural mortality rate be constant over the adult life span, the inference that rate of natural mortality varies with surrounding temperature may apply to these genera. The range in the mean environmental temperatures for the different North American stocks of Atlantic salmon is probably great considering the wide dispersal of their home rivers (MacCrimmon and Gots 1979) and the large latitudinal distance between the main marine feeding grounds in the Bay of Fundy and east of Newfoundland-Labrador (see Section 2.0).

The transition from fresh water to salt water is a physiological stress on Atlantic salmon smolts (Bakshtansky et al. 1979, 1980; Anon. 1983). Mortality attributed to osmoregulatory failure is unlikely considering the evidence that hatchery smolts survive either gradual or direct transfer from fresh water to seawater (Isaksson 1976b; Farmer et al. 1978). In studies of physiological and locomotory reactions of hatchery and wild smolts transferred to brackish water (13‰/00), Bakshtansky et al. (1979, 1980) found that hatchery smolts adapted slower than wild smolts. The difference recorded in adaptive capabilities would probably have been greater had the transfers been to full seawater (32‰/00). The increased physiological stress associated with adaptation to seawater would probably increase the salmon's vulnerability to predation and susceptibility to disease and parasites (Bakshtansky et al. 1979,

1980; Anon. 1983). Hatchery smolts would probably experience greater losses following entry to the estuary and sea since they adapt slower to seawater than wild smolts (Bakshtansky et al. 1979, 1980) and are less wary (Ginetz and Larkin 1976; Larsson 1985).

The impact of disease appears to be localized to a few North American salmon populations. Furunculosis (Aeromonas salmonicida) is present in salmon of the Restigouche River, New Brunswick, where it has annually since 1975 caused a mortality of between 3 and 24% of the large salmon entering fresh water (Randall et al. 1985a). This disease causes a loss of spawners in the river, but it is unknown whether it causes mortality among smolts or previous spawners entering the sea. Similarly, bacterial kidney disease, attributed to Renibacterium salmoninarum, appears to inflict negligible mortality in wild salmon except possibly within the population of the Margaree River, Nova Scotia, which is known to harbour the causative agent (Paterson et al. 1981; J. W. Cornick, Department of Fisheries and Oceans, Halifax, Nova Scotia, pers. comm.). Smolts having kidney disease lesions on internal organs (i.e., advanced state of the disease) experience low marine survival (Frantsi et al. 1975, 1977). Saltwater vibriosis, attributed to Vibrio spp. bacteria, has caused mortalities among salmon and other salmonids maintained in sea cages along the east coast of North America (J. W. Cornick, pers. comm.), but is not known to affect salmon ranging free in the sea. Tagged hatchery smolts vaccinated with a vibrio trivalent bacterin and released into Maine rivers yielded no difference in recapture rates than non-vaccinated controls (Baum et al. 1982).

3.3 ANALYSES AND RESULTS

3.3.1 Natural mortality between smolt and recruitment

Estimates of survival and natural mortality were determined for populations of Big Salmon and Sand Hill rivers. Survival was determined as the percentage of smolts that returned to the river or were caught in the sea fisheries as 1SW and MSW salmon. Natural mortality was estimated for the period between the smolt stage and sea age of 12 months. Except for incidental catches of post-smolts, sea age of 12 months represents the earliest that salmon first recruit to the fisheries.

3.3.1.1 Salmon of Big Salmon River

Survival and natural mortality rates were determined from numbers of smolts leaving the river from 1966 to 1971 and 1SW and MSW salmon returning to the river from 1967 to 1973 (Table 11).

Although 26% of the smolts were tagged between 1967 and 1971, the rates were determined for untagged smolts. Stock size at first recruitment was estimated by back-calculating river returns and losses to sea fisheries to sea age of 12 months, assuming a monthly natural mortality rate of 0.01 for salmon older than one sea-year (Doubleday et al. 1979).

Losses to the sea fisheries were estimated from tag recapture data for wild smolts marked with modified Carlin tags. Tag recaptures were partitioned by location and method of recapture, and sea age at first recovery (Table 12). Recaptures from the five smolt classes were pooled because recaptures from an individual smolt class were often few and no data were available for the 1966 smolt class. Annual variation in sea fisheries exploitation was not expected to significantly affect the estimates of survival and natural mortality since only 9% of the recaptures as 1SW and MSW salmon were made in the sea fisheries. Mortality caused by the sea fisheries was assumed to be represented by the mean proportions of the tagged salmon recaptured in the sea; sea fisheries accounted for 5% of the recaptures as 1SW fish and 18% of those recovered as 2SW and 3SW salmon. Harvests of salmon as smolts (2 tag recaptures) and post-smolts (35 recaptures) were assumed negligible and therefore included among losses attributed to natural mortality.

Recapture proportions for the sea fisheries were not adjusted for incomplete reporting of tags and non-catch fishing mortality since these losses were assumed to be compensated for by the incomplete counts of tagged salmon returning to the river. The small size of some recaptures as 2SW salmon in 1969 (i.e., fork length <63.5 cm or weight <3.0 kg) suggests that a number of them spawned previously in 1968, although no record of their return to the river as 1SW salmon exists. A high sport catch efficiency for tagged salmon returning to the river in 1969 (i.e., 19 of 25 recaptures reported in the river were made by the sport fishery) also indicates an incomplete count of tagged salmon returns to the river in 1969.

Survival and natural mortality rates were adjusted for handicap caused by the fence and counting operation. To estimate this handicap, the mean angling catches of grilse (i.e., maturing salmon of fork length <63.5 cm) for the periods 1967 to 1972 and 1974 to 1985 were compared (O'Neil and Swetnam 1984; Swetnam and O'Neil 1984, 1985; O'Neil et al. 1985, 1986). The main assumptions in this comparison are that angling exploitation and smolt production were the same for these two periods. The 1973 grilse catch was excluded since the counting fence was operated for a part of the smolt run in 1972. Grilse catches that would have been affected by the smolt fence operation were 62% of later catches. Tagging of smolts during the early years would have accounted for a major part of this

difference since tagged smolts yielded only 20 recaptures as 1SW salmon in the sport fishery while accounting for 26% of the smolt production from the river. The remaining difference between the average catches is assumed to represent the handicap caused by the fence and counting operation. A handicap ratio of 1.2 approximates this difference and was therefore used to adjust estimates of survival and natural mortality. A handicap of this magnitude seems realistic considering that known mortalities at the fence and in the trap ranged from 2.3 to 10.1% of the counted run (Jessop 1975). Numbers of smolts used to estimate survival include these losses plus delayed mortalities also caused by the fence and counting operation.

Table 13 contains the estimates of survival and natural mortality for the six smolt classes. Rates estimated for the 1967 smolt class were examined for bias because they varied considerably from those determined for the other five smolt classes. Bias is also suggested by the failure of the 1967 smolt class to produce a return of salmon commensurate with its high survival rate. The main area for potential bias lies with the estimate of the number of smolts migrating in 1967. The 1967 estimate was half of the average number of smolts migrating in the other five years (Jessop 1975). No estimate of counting fence efficiency was determined in 1967 although the count was adjusted to estimate the total smolt run by a factor comparable to that used in other years (Jessop 1975). If the number of smolts in 1967 equalled the average of the other five years, the survival of the untagged smolts (i.e., 21,872 minus 3900 tagged smolts) to the sea fisheries and return to the river would have been similar to the rate for the 1969 smolts (Table 13). In contrast, the combination of the survival rate determined for the 1967 smolts (i.e., 23.8%) with a smolt run equal to the 1970 run (i.e., 29,630) would yield a return of more than 6000 virgin 1SW salmon to the river. An annual production of this magnitude is unlikely considering that the average grilse catch in the river's sport fishery since 1973, which harvests roughly 25% of the return (Jessop 1986), is about 400 fish (O'Neil and Swetnam 1984; Swetnam and O'Neil 1984; O'Neil et al. 1985, 1986). The high survival rate determined for the 1967 smolt class appears to be either a biased estimate or an anomaly to the normal range in survival rates for this population.

The low survival rate determined for the 1968 smolt class (1.0%) seems reliable since the estimated number of smolts were largely (79%) based on the count at the fence (Jessop 1975) and the aged sample of 359 fish returning to the fence in 1969 (Table 11) should have provided an accurate estimate of 1SW salmon in the return. The 1968 smolts are presumed to have experienced an exceptionally high marine natural mortality since this trend of reduced abundance is also suggested by the low angling catch estimated for the Stewiacke, the other main upper

Bay of Fundy river (O'Neil and Swetnam 1984; Swetnam and O'Neil 1985). Low smolt survival does not appear to be unusual in these populations since exceptionally low grilse catches are also recorded for 1980 on both these rivers (Swetnam and O'Neil 1984).

Untagged smolts emigrating from Big Salmon River in 1966 and from 1968 to 1971 produced an average return of 6% as 1SW and MSW salmon to the river and sea fisheries (Table 13). Survival rates for these five smolt classes varied from 1 to 10%. Rates for three of the smolt classes were almost similar, ranging from 8 to 10% and averaging 9%. Losses to natural mortality in the first sea-year would in most years account for 90% or more of the smolts entering the sea. In some years, natural mortality is exceptionally high and according to the estimate for the 1968 smolt class may account for 99% of the migrants.

These estimates of natural mortality are exaggerated because they include losses of post-smolts to the fisheries. However, this bias is not expected to be large considering that only 35 recaptures as post-smolts were recorded from 30,542 tagged smolts.

3.3.1.2 Salmon of Sand Hill River

Estimates of survival and natural mortality were determined for the 1969, 1970 and 1971 smolt classes of the Sand Hill River population. Rates were derived from estimates of smolt numbers, counts of salmon returning to the river and tag recapture data used to estimate harvests by the sea fisheries (Pratt et al. 1974). The 1970 and 1971 smolt runs were determined from counts adjusted for fence efficiency while the 1969 run was estimated by mark and recapture (Murphy 1971; Pratt et al. 1974). According to these estimates, run totals for smolts (tagged plus untagged) in all three years were almost similar, ranging from 50,494 to 55,000.

Tag recaptures in both Canadian and Greenland sea fisheries were adjusted for a reporting rate of 0.8. The ICES Working Group on North Atlantic Salmon assumed rates of 0.9 for the Labrador fishery and 0.7 for fisheries along the Newfoundland and Nova Scotia coasts (Anon. 1986a). A reporting efficiency of 0.84 was estimated for the 1972 Greenland fishery (Jensen 1980). A non-catch fishing mortality rate of 0.1 was assumed for Greenland and Canadian fisheries. This rate is the minimum value assumed in the assessment of impact of the Greenland fishery on homewater stocks (Anon. 1981), and was applied to Canadian coastal fisheries when determining their effects on USA stocks (Anon. 1986a). A mean monthly natural mortality rate 0.01 was assumed for salmon older than sea age of 12 months when determining losses to natural mortality in the first sea year. This rate was

assumed in determining estimates for the Big Salmon River population and is the upper limit to the range of 0.005 to 0.01 suggested by Doubleday et al. (1979) for North American salmon. Survival and natural mortality estimates were not adjusted for possible handicap caused by the fence and counting operations because observed smolt mortalities were less than 1% (Murphy 1971, 1974). Estimates of the numbers of 1SW and MSW salmon produced by the untagged smolts are summarized in Table 14 by sea age and location of capture.

Among the three smolt classes, 20 to 27% of the untagged smolts survived to contribute to the sea fisheries or return to the river (Table 15). The average survival rate (23%) was 15 X the recapture rate for tagged smolts (1.5%) emigrating from the river in the same years. Losses to natural mortality in the first sea year ranged from 70 to 77%. Because estimates of survival and natural mortality are available for three smolt classes only, it is unlikely that the rates represent the full range of variation for the population.

3.3.2 Natural mortality between spawnings

Losses to natural mortality between spawnings were estimated for populations of the Big Salmon River and the LaHave River. These populations were selected for comparison because of their apparent difference in repeat spawning incidence (Cutting and Gray 1984; Jessop 1986) and availability of enumeration and aging data.

3.3.2.1 Spawners of Big Salmon River

Data used to estimate losses to natural mortality between spawnings included fence counts of salmon returning to the river from 1968 to 1972, sample aging data and sport fishery catch estimates. Estimates of returns to the river, available from Jessop (1986), were partitioned by using the grilse and large salmon breakdown and the aging data for the sampled returns of male and female salmon (Table 16). Since all repeat spawning occurred in consecutive years (Jessop 1986), estimates of natural mortality between spawnings were determined by comparing spawning escapements in year i with total returns to the river in year $i + 1$ from the same smolt classes, minus the virgin MSW salmon. Spawning escapement was estimated by subtracting the sport fishery catch from the estimated total return to the river. The sport fishery catch was assumed to account for all of the mortality between entering the river and spawning.

The uniformity of mortality rates among spawning classes, between sexes and with number of spawnings was examined by

pooling the data in Table 16 by these categories. Differences in mortality rates within categories were tested by weighted chi-square analysis (Snedecor and Cochran 1967). The normal deviate (Z) from regression analysis was used to assess the significance of linear trend in mortality rates with number of spawnings (Snedecor and Cochran 1967).

Mortality between spawning and return to the river in the following year varied among the four spawning classes from 23 to 78% and averaged 49% (Table 17). This variation was highly significant (chi-square = 807.2, df = 3, $p < 0.001$).

As estimates of natural mortality the losses are potentially exaggerated because of under-estimation of sport fishery catches upriver of the counting fence and assumptions that removals by poachers and in the sea fisheries were zero. Estimates of the upriver sport fishery catches should not have been greatly biased and losses to the marine fisheries were probably negligible considering that these fisheries accounted for only two tag recaptures from 72 1SW and older salmon that were passed through the counting fence and for which there are no reports of recapture in the sport fishery.

Male spawners experienced higher mortality between spawnings than females (58% versus 46%, chi-square = 16.91, df = 1, $p < 0.001$). Males disappeared from the aged samples after having spawned four times whereas females were recorded returning for the seventh time (Table 18). Both male and female spawners showed significant linear trends in mortality rate with number of spawnings (i.e., males, $Z = 10.3$, $p < 0.001$; females, $Z = 13.6$, $p < 0.001$).

3.3.2.2 Spawners of LaHave River

Numbers of salmon returning to LaHave River, 1978 to 1985, from wild smolts produced above Morgan Falls were used to estimate mortality between spawning and subsequent return to the river. Counts of grilse and large salmon at Morgan Falls provided estimates of spawning escapement since sport fishing is prohibited upriver of this point (Table 19). Losses to the sport fishery below Morgan Falls were determined using tag recapture data for hatchery smolts released above Morgan Falls and assuming that the fishery uniformly harvested wild and hatchery salmon homing to Morgan Falls. The resulting exploitation rates are minimal estimates since recaptures in the sport fishery were not adjusted for unreported tags. Sea age and spawning history were estimated for total river returns of wild salmon produced above Morgan Falls using scales from representative samples of grilse and large salmon taken at the counting trap (Table 20). Since both consecutive- and alternate-year spawners were present,

mortality was determined as the difference between the spawning escapement in year i and the sum of consecutive- and alternate-year spawners returning to the river in year $i + 1$ and year $i + 2$.

Estimates of mortality ranged from 73 to 93% (Table 21). Survival of the 1983 spawners was almost 4 X that of the 1981 spawners, which experienced the highest mortality of the six spawning classes, and almost 2 X that of the 1980 spawning class, which returned at the second highest rate. The high survival recorded for the 1983 spawning class is because of a high return of consecutive spawners in 1984 (i.e., they returned at more than 5 X the mean rate for the other five spawning classes). A reduced commercial fishing season in 1984 along the Nova Scotia coast may be partially responsible for the high survival recorded for the 1983 spawning class. An average return of consecutive spawners in 1985 (i.e., 3% of the 1984 spawning escapement), when no licensed commercial salmon fishery existed along the Nova Scotia coast, suggests that changes in the local commercial fishery were not solely responsible for the high survival of the 1983 spawners.

The estimated mortality largely represents the losses to the sea fisheries and natural mortality in both the river and the sea. The average mortality rate (86%) may approximate the total loss from spawning to subsequent return to the river under sea fishery conditions of the late 1970s and early 1980s. According to tag recaptures from hatchery smolts released into the LaHave River from 1978 to 1981, losses of MSW salmon to the sea fisheries in their return year are greater than 25% (i.e., 66 of 250 recaptures as 2SW and 3SW were returned from the sea fisheries). If the return migration of alternate-year spawners and virgin MSW salmon are similar, as suggested previously (see section 2.3.1.4), we might assume that sea fisheries reduce the return of alternate-year spawners by more than 25% since some previous spawners would also be caught during the year of re-entry to sea on their out-bound migration and possibly in the Greenland fishery. Even if losses to the sea fisheries in the year of re-entry to the sea equalled those of the return-year for alternate-year spawners, total losses to the fisheries experienced by the entire spawning class would be less than twice the losses incurred in the return-year since about half of the previous spawners returning to the river are consecutive-year spawners and therefore probably harvested only in local sea fisheries. By assuming that sea fisheries reduce the return of previous spawners by 25 to 50%, losses to natural mortality between spawnings were estimated to account for 72 to 82% of the original spawners. These estimates represent mortality between first and second time spawnings since calculations carried out after excluding the few older spawners provided similar values.

The losses to natural mortality are exaggerated because the estimates of sport fishery catches do not represent the total losses between entry to the river and spawning. Sport catches are underestimated since tag recaptures used to determine angling exploitation were not adjusted for incomplete reporting of tags. The sport catch estimates do not include losses to poaching or disease, both presumed to be negligible. Removals of salmon for hatchery broodstock are also unaccounted for, although wild salmon collected for the hatchery program were generally less than 5% of estimated spawning escapements and most were released after spawning. Considering these small biases it is likely that on average about three out of four spawners in the population die naturally between spawnings.

3.3.3. Smolt survival and migration time

Tagging data for both wild and hatchery smolts were examined for variation in recapture rates associated with times of migration and release. Recapture rates for the wild smolts were related to both tagging date and the minimum water temperature recorded at the site in the estuary where the smolts were trapped. The tagging date was used as an index of migration time since the wild smolts were trapped during their seaward migration. The comparison with minimum temperature was made because smolt survival was thought to be linked to estuarial temperature. Recapture rates for hatchery smolts were compared with the date of their release into the headwaters of a river situated near the hatchery. Both wild and hatchery smolts were marked with modified Carlin tags (Saunders 1968). The hatchery smolts were tagged at least one month prior to their release.

3.3.3.1. Wild smolts

The wild smolts tagged were a subsample of those caught in an estuarial trap at Millbank on the Miramichi River. Although smolts from this trap were tagged in each of nine years from 1968 to 1976, insufficient data limited analyses to data from five years.

Relative survival rates for smolts were expressed as the proportion recaptured as 1SW and older salmon from smolts tagged on a particular day. Recaptures were mainly from the sea and river fisheries and do not include all those in spawning escapements. Although smolts were generally tagged on the date of capture, occasionally they were retained in live boxes one to three days before tagging. This irregularity was not always documented, and therefore its potential effects were ignored in analyses and the resulting error was assumed to be random. Tagging and recapture data with tagging dates and measurements of

estuarial temperatures are summarized in Table 22.

Weighted regression analysis similar to that described in section 2.3.2.2 was used to compare recapture rates with tagging date and estuarial temperature. Tagging date was designated by the Julian day. Estuarial temperature was represented by the minimum temperature since the previous day. Both linear and parabolic regression models were used to assess the potential relationships between smolt survival and either migration time or estuarial temperature. Data from each smolt class were assessed separately because of large annual variation in recapture rate (i.e., annual rates ranged from 1.3 to 2.9%) and anticipated difference among years in date of migration.

Significant ($p < 0.10$) regressions between recapture rate and tagging date were recorded for all five smolt classes (Table 23). Three of the regressions were parabolic and two were linear (Fig. 2). The parabolic relationships show a common tendency whereby recapture rates were greatest for smolts tagged in early June. The linear relationships of the 1974 and 1975 smolt classes also indicate a decline in recapture rate for smolts tagged after the first week in June. Recapture rates for the 1974 smolt class should not be expected to vary parabolically in relation to tagging date since no smolts were tagged prior to June 6. Recapture rates for the 1975 smolts varied from the common parabolic tendency as a result of higher than expected rates produced by smolts marked on the first two days of tagging (i.e., May 26 and 27).

Significant ($p < 0.10$) regressions between recapture rate and minimum temperature were recorded for three of the five smolt classes (Table 23). The regressions were linear and showed a progressive decline in recapture rate as estuarial temperature rose. It is unlikely that smolt survival varies directly with estuarial temperature considering that recapture rates for two of the five smolt classes were not significantly correlated with temperature and that temperature was highly correlated with tagging date (i.e., r -values range from 0.74 to 0.94). As well, two of the three linear regressions with minimum temperature were with the same recapture data sets that were linearly related to tagging date.

3.3.3.2 Hatchery smolts

Thirteen groups of tagged hatchery smolts were released between 1978 and 1981 into the LaHave River above Morgan Falls. The releases span the six week period from April 23 to June 4. The release groups were comprised of 1+ smolts which were native to the LaHave River. All smolts were produced at Mersey Hatchery (Goff and Forsyth 1979). The smolts were large grade with mean

fork length of the release groups varying from 16.5 to 19.1 cm. Recaptures of tagged smolts included 1SW and older salmon recovered in sea or river fisheries, or returning to a counting trap in the Morgan Falls fishway which is situated down river of the release sites. The relationship between recapture rate and release date was examined using the weighted regression procedure described in section 2.3.2.2. Tag recapture and release information are summarized in Table 24.

The regression between recapture rate and release date was parabolic ($F = 8.05$, $df = 2,10$, $p = 0.009$) with highest recapture rates for smolts released in the first two weeks of May (Fig. 3). Most of the scatter about the fitted regression (84%) seems attributable to yearly difference in recapture rate and variation in smolt length as indicated when these variables were included in the regression. The higher loss experienced by smolts released in April and after mid-May could have occurred in the river as well as in the estuary and sea, since all smolts were released more than 25 km above the head of tide.

3.3.4 Failure of the 1977 smolt class

Recreational and commercial catches of salmon were examined by size class and location to determine the reduction in survival experienced by smolts entering the sea in 1977 and the geographic distribution of North American populations affected similarly. The reduction in survival was estimated by comparing the 1978 and 1979 catches of small (mainly 1SW salmon) and large (mainly 2SW salmon) salmon with the means of catches in the four most immediate years. The catch years forming the base for these comparisons were selected because they encompassed a period when there were minimal changes in Canadian fisheries regulations pertaining to Atlantic salmon and when the effects of the Greenland fishery on 2SW salmon returns to North American waters would have been relatively constant, i.e., Greenland catch was relatively constant from 1976 to 1980 (Anon. 1986b). Percent anomalies between recreational catches produced by the 1977 smolt class and the means of base-year catches were assumed to represent the difference in smolt-to-recruit survival. The same comparisons were made of catches for the commercial fisheries and are provided as an indicator of their possible effect on river escapements. Patterns in commercial fishery catches might not coincide with trends in salmon abundance in local rivers since the commercial fisheries generally harvested a mixture of salmon produced both locally and originating from distant rivers (Marshall 1982; Pippy 1982; Meister 1984; Anon. 1986a).

Abundances of 2SW salmon were designated more precisely in two areas than by the numbers of large salmon. One area is the State of Maine for which the index of abundance was designated by

catches of 2SW salmon (Anon. 1986a). The angling catches of wild 2SW salmon of the Narraguagus River were assumed to be more representative of relative survival rates than were total catches of large salmon in the State's sport fishery because of the impreciseness of age designation by fish size and the variable contribution made by hatchery smolts. The second area is Quebec for which large salmon catches in the recreational fisheries were limited to salmon ≥ 2.2 and < 5.4 kg. Exclusion of salmon ≥ 5.4 kg eliminated most previous spawners and virgin 3SW salmon common to some Quebec populations (Schaffer and Elson 1975). Large salmon catches in upper Bay of Fundy areas were excluded from analyses because they are comprised largely of previous spawners (Amiro and McNeill 1986; Jessop 1986). Similarly, recreational catches of large salmon numbering less than 10% of an area's total catch were excluded because of the likelihood that many were previous spawners. Catches on Prince Edward Island were excluded because its rivers produce few salmon and catches were low. Salmon taken as by-catch were excluded except when combined with larger catches in licensed salmon fisheries. Catches of small salmon in commercial fisheries of Nova Scotia were excluded because they were mainly by-catch.

According to the comparisons of recreational catches not all North American rivers experienced reduced returns from the 1977 smolt class, but in those that did, catches were often less than 50% of base-year catches (Table 25). This tendency of reduced catches was common to populations of Maine, almost all rivers in Nova Scotia and New Brunswick, the Gaspé and Anticosti areas of Quebec, Areas N, M, K, J₂, F and A of insular Newfoundland and southern Labrador. Exceptions were noted for populations of the upper Bay of Fundy, the lower North Shore of Quebec, Ungava Bay, northern Labrador and most rivers on the east and south coasts of Newfoundland. These exceptions did not seem linked to low exploitation by the sea fisheries. Average recruit abundance recorded for several areas of Newfoundland might apply only to the 1SW salmon since no comparable estimates were available for 2SW salmon in all but Area K.

Recreational catch anomalies for small and large salmon originating from the 1977 smolt class were consistent in all but one of fifteen areas in which both sea-age classes were harvested. This exception, recorded for salmon of the upper North Shore of Quebec, indicated that catch of 1SW salmon was average while that of 2SW salmon was half the average. A reduced return of 2SW salmon to this area is also suggested by the low catch of large salmon in the local commercial fishery. An average recreational catch of 1SW salmon for the upper North Shore in 1978 is consistent with that for the adjacent lower North Shore.

The difference between anomalies for the total recreational

catches of small and large salmon (i.e., -29 versus -66%) is attributed mainly to the difference in geographic distributions of small and large salmon catches. All but 2% of the large salmon sport catches originated from mainland rivers where most populations experienced reduced returns of 2SW salmon in 1979. More than 80% of the small salmon sport catch was recorded in rivers on insular Newfoundland where average or greater catch in 1978 was common to nine of the fifteen areas.

3.3.5 Effects of marine temperature on recruitment

Indices of smolt-to-recruit survival were examined in relation to SST during the post-smolt year. Survival indices were comprised of recreational catches of grilse for two populations and a series of survival rates between the smolt stage and recruitment as 1SW salmon. The populations were of the Big Salmon and Stewiacke rivers of the upper Bay of Fundy, and of Western Arm Brook, Area N, Newfoundland. The upper Bay of Fundy populations limit their migrations to the area in and about the Bay of Fundy (see section 2.0), whereas the Western Arm Brook population migrates to and from the northwest Atlantic east of Newfoundland (Chadwick et al. 1985). Grilse catches in upper Bay of Fundy rivers were related to Bay of Fundy SST while survival rates for smolts from Western Arm Brook were regressed against temperature conditions in the northwest Atlantic. A linear regression model was used to explore these relationships.

3.3.5.1 Upper Bay of Fundy salmon

The index of 1SW salmon abundance for the Stewiacke River population is the total grilse catch in the river's recreational fishery (Table 26). Recreational catch of grilse from June to September was chosen as the index of 1SW salmon production from Big Salmon River (Table 26). Catch series for both populations extended from 1970 to 1985. October catches were excluded from the catch series for Big Salmon River because season closure varied between September 30 and October 31, and the October catch accounted for less than one third of the total catch in any year. Although season closure date varied on the Stewiacke River between October 15 and October 31, October catches were included since they often accounted for more than 50% of the total catch and because records did not permit partitioning of catches beyond monthly totals. The mean of catches for the six years in which the season was extended beyond October 15 on the Stewiacke River (439) was less than the mean for the other ten years (541).

The 1970 to 1973 catches for the Big Salmon River were adjusted upwards to compensate for handicap attributed to the trapping and counting of the smolts which produced the returns in

those years, and for differential mortality experienced by the smolts which were tagged. The first step in this adjustment was to determine the catches of grilse originating from untagged wild smolts. These were estimated by reducing grilse catches by the reported catches of tagged 1SW salmon originating from both wild and hatchery smolts. Catches were further reduced to account for a tag loss of 25% (Isaksson and Bergman 1978). The 1970 to 1972 catches originating from untagged smolts were adjusted upwards by the proportions of the wild smolt runs that were tagged in the previous year (28 to 33%) and also by a handicap ratio of 1.2 to compensate for the differential mortality caused by smolt trapping and counting (see section 3.3.1.1 for explanation). Similar adjustments were made to the 1973 catch except that a lower handicap ratio of 1.1 was used because the 1972 smolt counting operation was incomplete and only about half as many smolts were counted as in the previous three years (Jessop 1975).

Catches on the Stewiacke River in 1984 and 1985 were adjusted to compensate for a change in the method by which sport fishery catches have been estimated for Nova Scotian rivers. Beginning in 1984 catches were estimated using a license stub-return system rather than from creel surveys conducted by field officers of the Department of Fisheries and Oceans. Catches reported for 1984 and 1985 (O'Neil et al. 1985, 1986) were reduced by 32% to adjust for the difference in estimates reported by field officers and determined from the stub-return system. This adjustment factor is based on a comparison of paired estimates of total catches determined independently by the two methods for the Stewiacke in 1983 and 1984 (S. F. O'Neil, Department of Fisheries and Oceans, Halifax, Nova Scotia, pers. comm.).

Catches were regressed against both river flows during the harvest period and SST in the post-smolt year (Table 26). The variable river flow was introduced into the regression to compensate for the effects of varying river discharge on catch rate. Since records of flow were not available for Stewiacke and Big Salmon rivers, relative rates of discharge were assumed to be represented by measurements on the nearby Musquodoboit River, Nova Scotia, and the Point Wolfe River, New Brunswick, respectively. Mean flows were determined from daily recordings at gauging stations maintained by the Inland Waters Directorate, Environment Canada (Anon. 1985d, 1986c). Measurements of SST for the Bay of Fundy were represented by monthly means determined from twice daily recordings at the Biological Station of the Department of Fisheries and Oceans, St. Andrews, New Brunswick (45° 05'N, 67° 03'W). Analyses did not include the 1986 catches because of missing temperature measurements and uncertain record comparability after the change-over to a continuous temperature recorder in 1985.

The first step in analyses involved the regression of catches against mean river flows. The Big Salmon catches of grilse were regressed against mean flows for July through September. Few grilse are caught earlier than July on Big Salmon River. Stewiacke catches of grilse were regressed against mean flows both for September 1 to October 15, and for September 1 to season closure. Catches prior to September on the Stewiacke generally accounted for less than a quarter of annual grilse catches. Only the regression of Big Salmon catches on corresponding mean flows for the Point Wolfe was significant ($p < 0.05$). Flow was expected to have a direct effect on Big Salmon catches since mid-season closure of the angling fishery from a few days to two months was frequently invoked on this river because of low flows. The non-significance ($p > 0.05$) of either flow variable in regression with Stewiacke catch probably reflects the lateness of the main harvest (i.e., late September and October) when flows are generally greater than during summer.

To identify potential temperature variables, the residuals from the regression of Big Salmon catches on flow and grilse catches for the Stewiacke were compared with monthly means of SST from June to May of the first sea-year. Recruitment indices for both populations were negatively correlated to SST for June through October. Highest correlations were with early-summer SST. The mean of sea temperatures during June and July was therefore selected as the temperature variable. Suggested correlations with monthly mean sea temperatures for August to October were attributed to apparent correlations between monthly temperature series.

Grilse catches on the Big Salmon ($CATCH_{BS}$) varied positively with mean flow rate for the main catch period ($FLOW$) and negatively with mean sea temperature for June and July of the post-smolt year (SST). The two variables accounted for 74%

$$CATCH_{BS} = 1971.1 + 96.33 \overline{FLOW} - 167.48 \overline{SST}$$

of the variation in grilse catch between 1970 and 1985. $\overline{SST}$ accounted for 46% of the variation in recruitment (Fig. 4). The June-July period of sensitivity to sea temperature coincides with time of entry and early life in the sea. Jessop (1975) reported the timing of the smolt run on Big Salmon to be late May through early June.

Grilse catches on the Stewiacke ($CATCH_{STEW}$) also varied negatively with $\overline{SST}$ (Fig. 4). Fifty percent of the variation

$$CATCH_{STEW} = 4615.0 - 364.67 \overline{SST}$$

in catch was associated with the annual variation in sea temperature. The grilse catch for the Stewiacke River was also significantly correlated with the recruitment index for the Big Salmon population (i.e., $r = 0.559$, $df = 14$, $p = 0.024$).

3.3.5.2 Western Arm Brook salmon

Annual variation in smolt-to-recruit survival among smolt classes 1971 to 1983 of Western Arm Brook was related to three of the five indices of SST for the northwest Atlantic which were used to investigate SST effects on sea distribution and exploitation of Saint John River salmon (see section 2.3.3.2). These variables as previously designated are: i) the latitude ($^{\circ}N$) of the northward extent in January of the $4^{\circ}C$ isotherm west of $45^{\circ}W$ (VAR1); ii) the area ($km^2 \times 1000$) covered by $4^{\circ}C$ or warmer water in January north of $50^{\circ}N$ and west of $40^{\circ}W$ (VAR3); and iii) the Julian day on which the $0^{\circ}C$ isotherm receded north of $50^{\circ}N$ along the Newfoundland east coast (VAR5). VAR1 and VAR3 (Table 10) were presumed to represent the severity of winter conditions in the northwest Atlantic, whereas VAR5 (Table 8) was assumed to indicate spring sea temperature conditions along the Newfoundland east coast. VAR2 and VAR4 (Table 10) were excluded from this analysis because they refer to the west coast of Greenland where North American salmon destined to mature as grilse are not known to frequent (May 1973).

Survival was determined as the proportion of smolts emigrating from Western Arm Brook that either returned to Western Arm Brook or were caught in the commercial fisheries. Numbers of smolts and returns of 1SW salmon to Western Arm Brook were based on fence counts (Table 27). Numbers of 1SW salmon caught in the commercial fishery were estimated as 20% of the commercial harvest in Area N (Table 27). This method of estimating the commercial harvest was proposed by Chadwick (1984) on the assumptions that smolt production in Western Arm Brook was 10% of the total for Area N, and harvest in distant fisheries was equal to harvest in the Area N commercial fishery. The smolt production estimate is based on the relative sizes of drainage areas for Western Arm Brook and all rivers in Area N. The assumption of equal harvest in Area N and distant fisheries was based on tagging studies involving previous spawners which indicated about equal recaptures in the commercial fishery in Area N and the more distant fisheries (Chadwick et al. 1985).

A weighted linear regression model, similar to that described in section 2.3.2.2, was used to determine possible relationships between survival and the three SST variables.

Smolt-to-recruit survival of Western Arm Brook salmon was related to both VAR1 ($F = 11.675$, $df = 1,11$, $p = 0.006$) and VAR3

($F = 9.030$, $df = 1,11$, $p = 0.012$), but not VAR5 ($F = 0.055$, $df = 1,11$, $p = > 0.5$). VAR1 and VAR3 are highly correlated ($r = 0.880$, $df = 11$, $p < 0.001$) and both are measurements of the severity of winter conditions in the northwest Atlantic. The significant regressions indicate that Western Arm Brook post-smolts experienced progressively higher survival when warm sea temperature conditions during winter prevailed farther north in the northwest Atlantic (Fig. 5).

The largest residuals in both significant regressions were recorded for the 1977 smolt class. Predicted survival rates (0.121, 0.128) were twice the rate (0.059) determined for this smolt class. Despite the magnitude of these residuals, winter temperature conditions in the northwest Atlantic were conducive to below average survival for the 1977 smolt class (Fig. 5).

3.3.6 Effects of forage availability on recruitment

The possibility that post-smolt survival varies with forage availability was investigated by comparing survival with indices of post-smolt growth. This indirect approach was selected because diets of salmon in the sea vary (Lear 1980) and indices of forage abundance are not available. Salmon seem to be opportunistic feeders (Lear 1980) and hence a low abundance of a particular food item (e.g., capelin) should not affect survival if alternate forage were available.

Indices of post-smolt growth for the 1977 smolt class were compared with corresponding measurements of growth for smolts entering the sea in other years. The comparisons were based on fork length and growth measurements for both wild and hatchery 1SW salmon returning to Morgan Falls, LaHave River. Smaller adult fork length or lower growth rates were expected of the 1977 smolt class if reduced forage availability contributed directly to their lower survival. According to recreational and commercial fisheries catches (southwest shore, Nova Scotia, Table 25) and tag recapture rates for hatchery smolts (0.18% for 1977 smolts versus 1.92% for 1976, 1978 and 1979), survival rates for smolts from the LaHave in 1977 were 50% or less of those experienced by other smolt classes of the mid to late-1970s.

Four of the five indices of sea growth were estimated by back-calculation using counts of circuli and measurement of radii along the longest axis of the scale (Lear and Sandeman 1980). The five indices are: 1) fork length at return; 2) fork length increment between smolt stage and return; 3) mean fork length increment per circulus spacing between smolt stage and return; 4) mean fork length increment per circulus spacing during summer-fall of first sea-year (i.e., for first 16 circuli of sea growth); and 5) mean fork length increment per circulus spacing

during winter-spring (i.e., for final 20 circuli of sea growth). Selections of cut-off points for growth phases of summer-fall (first 16 circuli) and winter-spring (final 20 circuli) were based on a preliminary examination of scales from LaHave salmon. This method of determining the cut-off points for these growth phases was less biased than subjectively deciding for each scale where the winter phase began.

Indices of growth were determined for samples of 25 1SW salmon that returned to Morgan Falls before mid-July. This selection of early-returning fish was aimed at minimizing the variation in sea growth after the winter.

Difference between measurements of sea growth was determined by analysis of factor effects and the Bonferroni method of multiple comparisons (Neter et al. 1985). The significance of difference between pair-wise comparisons was based on 95% confidence intervals.

The analysis was carried out in two stages. The first involved the five indices of sea growth, with comparisons made between the 1977 smolt class and 1978 and 1980 classes, respectively. Replication of comparisons was satisfied through independent sampling of returns originating from wild and hatchery smolts. The 1978 and 1980 smolt classes were selected for this analysis on the basis of availability of scale samples which were scarce in some years for returns from hatchery smolts. To eliminate potential effects of smolt age, samples were taken only from 1SW salmon originating from 2+ wild and 1+ hatchery smolts. Survival rates for 1978 and 1980 smolt classes seemed average according to local fisheries catches (Cutting and Gray 1984) and tag recapture rates for hatchery smolts (i.e., 1.65 and 1.72%, respectively).

In the second stage of the analysis, the index of growth that depicted the most consistent difference between the 1977 smolt class and the other two classes, was investigated further. In this analysis the 1977 smolt class was compared against smolt classes 1976 and 1978 to 1986. This analysis was limited to measurements for wild 1SW salmon since sufficient scale samples for hatchery salmon were not available for several smolt classes.

Of the five indices of sea growth investigated, only summer-fall growth rate of the 1977 smolt class was consistently different. One-sea-winter salmon of the 1977 smolt class grew less during the summer-fall period than did representatives of the 1978 and 1980 smolt classes (Table 28). This tendency, common to both hatchery and wild salmon, reflected a general reduction rather than interruption in growth during the summer-fall period, since scales from the 1977 smolt class showed no abnormal check(s). Pair-wise comparisons indicated

significant difference ($p < 0.05$) between summer-fall growth rates for the 1977 smolt class and the 1978 and 1980 smolt classes. In spite of differences in summer-fall growth rates, the three smolt classes varied less than 2 cm in mean annual sea growth within hatchery and wild population components.

Comparisons to include eight more smolt classes of wild salmon confirmed the irregularity of summer-fall growth experienced by the 1977 smolt class (Table 29). All other smolt classes experienced greater average instantaneous rates of summer-fall growth. Average length increases during the summer-fall period for the ten other smolt classes were 0.85 to 1.95 cm greater.

3.3.7 Effects of predation on recruitment

Considering that predation is believed to account for most of the natural mortality in the sea (Cushing 1974; Ricker 1976; Doubleday et al. 1979), it is likely that recruitment rates are affected by local and annual abundances of predators.

3.3.7.1 Cormorants

Attention was drawn to predation by double-crested cormorants (*P. auritus*) on salmon smolts or post-smolts when an angler returned 126 modified Carlin tags (Saunders 1968) that were reported to have been recovered on July 2, 1986, from a cormorant rookery on Tobacco Island, Nova Scotia (Fig. 6). A subsequent search of the same rookery by DFO personnel on July 21, produced additional tags thereby supporting the previous report. A search of a second rookery, on Indian Island, Nova Scotia (Fig. 6), on August 6, also yielded salmon tags. The two rookeries are separated by more than 300 km of coastline.

The tags recovered from both rookeries by DFO personnel were found on the forest floor below the trees supporting nests of cormorants. The search for tags involved removing the guano covered surface layer of twigs and then raking the underlying spruce needles with a small hand rake. Most tags were found among the surface twigs. A search time of about 12 hours in each of the rookeries yielded 33 tags at each location. Searches did not cover the entire rookeries and their efficiencies are unknown.

The 192 tags recovered from the two rookeries originated from hatchery smolt releases into four different rivers (Table 30). Ninety-one percent of the tags were from the 1986 releases. The other tags originated from releases in previous years and as early as 1981. All tags came from rivers which emptied into the

sea within 20 km of the respective rookeries.

Seventy-six percent of all tags recovered from the two rookeries were from a release of 5987 smolts stocked in the St. Mary's River in 1986. This represents a minimum predation rate of 2.4%. Ninety-seven of the 146 tags from the 1986 release into the St. Mary's River were from 2995 smolts stocked May 20 in the west branch of the river. The remaining 49 tags were from 2992 smolts released May 26 in the east branch. These data suggest that the breeding colony on Tobacco Island consumed twice as many smolts from the earlier release in the west branch as from the later release in the east branch.

3.3.7.2 Cod and grey seals

Evidence that cod and grey seals are predators of salmon is based on several reports that they prey on salmon (Rae 1968; Soderberg 1975; Mansfield and Beck 1977; Larsson 1980; Anon 1983; Hvidsen and Møkkelgjerd 1987) and observations that they consume large biomasses of fishes, including the pelagics (Mansfield and Beck 1977; Lilly 1986).

Assessments of the Atlantic cod stocks south of NAFO Division 2H and within Canada's 200 mile limit indicate that biomasses of cod larger than 1.5 kg in these areas have increased by more than 100% between the mid-1970s and mid-1980s in all but NAFO Division 4X, and by more than 400% in some Divisions (Fréchet 1987; Baird and Bishop 1988, 1989; Chouinard and Sinclair 1988; Fanning et al. 1988; Campana and Hamel 1989). Cod larger than 1.5 kg (ages 4+ to 7+ depending upon location) could consume salmon post-smolts of a wide range of sizes (Ursin 1973; Anderson and Ursin 1977).

Grey seals have also increased in abundance (Mansfield and Beck 1977; Zwanenburg 1984). The population of grey seals in eastern Canada may have exceeded 100,000 animals in 1983 (Zwanenburg 1984). Pup production on Sable Island, the largest breeding colony for grey seals in eastern Canada, increased annually by 12% since 1962 (Zwanenburg 1984). This rate of increase has continued through 1984 and 1985 (K. Zwanenburg, Department of Fisheries and Oceans, Halifax, Nova Scotia, pers. comm.). According to estimates based on pup production and age distribution data, the grey seal population of eastern Canada has increased 400 to 500% between 1972 and 1986 (Zwanenburg 1984; K. Zwanenburg, pers. comm.).

Nine series of recreational catches of grilse and one series of survival rates for wild smolts were regressed against year of catch to assess the possibility of inverse relationship with apparent increases in cod biomass or the number of grey seals.

This indirect approach to assessing the effects of predation was selected because all but one of the potential predator populations, referred to previously (i.e., cod stock in Division 4X), increased in abundance since the early or mid-1970s.

The nine series of recreational catches are detailed in Table 31. They span catch years 1972 to 1985 (1 series) or to 1986 (8 series). They include catches in two upper Bay of Fundy rivers, the Miramichi River and the collective catches of most rivers in Quebec and Newfoundland-Labrador. These latter catches were grouped under six areas. Catches in other areas were excluded because of incomplete or unreliable data, changes in the impacting fisheries or deterioration in habitat. Only grilse catches were used because recreational catches of large salmon have been affected during the 1980s by changes in both commercial and recreational fisheries (Anon. 1987, 1988).

The series of survival rates is for the Western Arm Brook population and spans smolt classes 1971 to 1983 or correspondingly catch years 1972 to 1984. The method by which survival rates were estimated is described in section 3.3.5.2 and the data used to derive the rates are detailed in Table 27. Since the rates are proportions, a weighted regression model similar to that described in section 2.3.2.2, was used.

Because of the different time periods over which cod and grey seal populations have demonstrated growth, the indices of recruitment were regressed against catch years from both 1972 and 1977 to 1984, 1985 or 1986, depending upon the data series.

The nine series of grilse catches show no significant decline with time ($p > 0.05$) since the early or mid-1970s. This is also reflected by correlation coefficients (r) that are either nonsignificant ($p > 0.05$) or positive (Table 31). Similarly, the regressions of survival rate for the Western Arm Brook population on catch year indicate no decline with time ($p > 0.05$). The ten series are representative of a wide distribution of river populations extending from the Bay of Fundy to Labrador. The results are contrary to those expected had expanding cod or grey seal populations affected recruitment success of North American salmon on a major scale.

The catch series for rivers along the south coast of insular Newfoundland shows a constant and significant ($p < 0.05$) increase since both the early and mid-1970s (Table 31). Similarly, the series for the east coast of Newfoundland indicates an increase in catch since the early 1970s but is unchanged since the mid-1970s. Whether these increases reflect enhanced recruitment success in these areas or changes in exploitation in the recreational or commercial fisheries is unknown. Regardless, these trends do not alter the conclusion that no major decline in

recruitment has occurred since the early 1970s.

3.4 DISCUSSION

The average survival rate of smolts from the Sand Hill River (23%) was more than 3 X the average (6%) and twice the maximum rate (10%) determined for the Big Salmon River population. Corresponding estimates of natural mortality suggest that the Big Salmon smolts experience about a 20% greater loss in the first 12 months of sea life than do migrants from the Sand Hill (i.e., 93.7 vs 73.6%). Although the precision of individual estimates of survival rates may be questionable, the large difference between the two populations seems credible. The high rates estimated for the Sand Hill population are consistent with an estimate made by Chadwick et al. (1985) for Western Arm Brook salmon, which also feed in the Northwest Atlantic. They estimated that a minimum of 16.5% of the 1976 smolts emigrating from Western Arm Brook survived to contribute to the sea fisheries or return to the river as 1SW salmon. In contrast, low survival rates for Big Salmon smolts seem reasonable considering that the coupling of northern population survival rates of 16.5 to 26.7% with Big Salmon smolts runs of 13,400 to 29,600 (Jessop 1975) would result in angling catches (assuming an exploitation of 25%) that are 1.2 to 4.4 X the average annual catch recorded from 1975 to 1985 for Big Salmon (O'Neil and Swetnam 1984; Swetnam and O'Neil 1984; O'Neil et al. 1985, 1986).

Survival rates for the Sand Hill population would be exaggerated if smolt numbers were underestimated; a 20% underestimation would reduce the average survival rate from smolt to first recruitment to 21.1%. Such an underestimation is unlikely considering both the similarity in smolt numbers in each of the three years (50,474 - 55,000) (Pratt et al. 1974) and absence of any evidence of bias (Murphy 1971, 1974; J. D. Pratt, Department of Fisheries and Oceans, St. John's, Newfoundland, pers. comm.). In contrast, the assumption that the fence and counting operation had no effect on the survival of the unmarked smolts may have contributed to underestimation of the survival rates. Similarly, both the 0.8 reporting rate for the return of tags from sea fisheries and the 0.1 non-catch fishery mortality rate assumed for all sea fisheries are probably minimum rates. It is probable that the average survival rate between smolt and first recruitment for the Sand Hill population is indeed greater than 20%.

The observation that smolt-to-recruit survival rates for the Big Salmon population are lower than for the Sand Hill population is consistent with the relationship demonstrated by Pauly (1979) that fish stocks which occupy warmer waters experience higher

natural mortality than those living in colder waters. Although precise temperatures are unknown, salmon of Big Salmon probably live in warmer water than do Sand Hill salmon, considering the latitudinal differences of their river mouths ($45^{\circ} 25' N$ versus $53^{\circ} 32' W$) and their main feeding areas in the sea (Bay of Fundy and neighbouring areas versus Labrador Sea and Davis Strait) (Pratt et al. 1974; section 2.0).

Smaller smolt size may have contributed to the lower survival rates recorded for the Big Salmon population. Big Salmon smolts ranged from 13.6 to 15.1 cm in annual mean fork length and were generally at least 1 cm smaller than Sand Hill smolts (Murphy 1971, 1974; Pratt et al. 1974; Jessop 1975). Several studies indicate that survival varies directly with smolt size (Hager and Noble 1976; Isaksson 1976a; Larsson 1977b; Ritter 1977; Bilton 1984; Ward and Slaney 1988). The smaller smolt size of the Big Salmon population is common to other populations including those of the Northwest Miramichi (Forsythe 1967) and the Gulf of Maine (Bigelow and Schroeder 1953). In contrast, the Western Arm Brook smolts, which experience high survival rates (Fig. 5), exceed 16 cm in mean fork length (Chadwick 1987).

The difference between survival rates for Big Salmon and Sand Hill populations is likely related to their different sea distributions and may reflect an overall difference in the survival characteristics of upper Bay of Fundy salmon and other North American populations. When extreme high and low survival rates for smolt classes are excluded, 8 to 10% of the upper Bay of Fundy smolts may be expected to survive to sea age of 12 months. A comparable survival rate for northern populations of Labrador and insular Newfoundland is about 20% and perhaps greater for some.

The estimates of natural mortality between spawnings for populations of Big Salmon and LaHave rivers represent losses in both the river (during and following spawning) and the sea. Murray (1967) reported a mean survival of 73% between spawning and departure from the Little Codroy River, Area K, Newfoundland. Similarly, Chadwick et al. (1978) accounted for 88% of the 1973 upstream migrants of 1SW salmon in Western Arm Brook in a count of the following spring's sea-bound previous spawners. Although the same authors reported lower survival rates for other spawning classes, these other estimates are potentially biased because of incomplete counts of previous spawners (E. M. P. Chadwick, Department of Fisheries and Oceans, Moncton, New Brunswick, pers. comm.). Regardless, partitioning of natural mortality experienced by previous spawners between losses in the river and the sea seems meaningless since most losses are likely attributable to reduced physiological condition from long fasting associated with spawning (Belding 1934). Re-initiation of

feeding and re-acclimation to salt water would presumably be stressful to previous spawners depleted of their energy reserves and in a weakened state. Most of the mortality probably occurs before and during early re-conditioning since predation should be negligible on previous spawners considering their large size (Cushing 1974; Mathews and Buckley 1976; Ricker 1976; Doubleday et al. 1979).

The difference between natural mortality rates estimated for Big Salmon and LaHave populations typifies a main difference in the life history characteristics of salmon from upper Bay of Fundy rivers and other areas of North America (Schaffer and Elson 1975; Amiro and McNeill 1986; Jessop 1986). Estimates that 18 to 28% of the previous spawners from the LaHave survive to be caught in sea fisheries or return to the river are probably representative of most North American populations. Even previous spawners of the Sand Hill population, which comprise 10% of the large salmon and less than 1% of all salmon returning to the river (Pratt et al. 1974), probably survive similarly to LaHave previous spawners, particularly if they are heavily exploited like the virgin 2SW salmon of the Sand Hill. According to estimates of catches and returns to the Sand Hill (Table 14), 814 2SW salmon returned to the river from three smolt classes while 11,127 2SW salmon were harvested in Canadian commercial fisheries (i.e., an exploitation of 93%). Previous spawners of the Sand Hill are probably exploited as well on their outbound migration and at Greenland. Some previous spawners of the Sand Hill population are caught at Greenland (T. R. Porter, Department of Fisheries and Oceans, St. John's, Newfoundland, pers. comm.), as expected, since about 95% of those spawning more than once are alternate-year spawners (Pratt et al. 1974).

Salmon of upper Bay of Fundy rivers experience greater natural mortality between smolt and recruitment and lower natural mortality between spawnings than other North American populations. This life history strategy appears unique to those populations which are believed to limit their sea distribution to the Bay of Fundy area (see section 2.0).

Natural mortality between spawnings experienced by salmon of the Big Salmon River varied annually, and with sex and number of spawnings. The annual variation may reflect varying environmental conditions in both the river and the sea. The trend for natural mortality to increase with each successive spawning is characteristic of senescence (Comfort 1979). The tendency for males to experience higher natural mortality between spawnings than females is consistent with reports for European and other North American populations of Atlantic salmon (Lévesque et al. 1985).

The parabolic relationship between recapture rate for

Miramichi wild smolts and the time of their migration through the estuary may be biased by variable handling effects. Jessop (1975) reported that mortality from handling stress was greater among wild smolts migrating late and when water temperature was high. Despite this, it is unlikely that handling effects caused all the decline in recapture rate for the wild smolts migrating after the first week in June, since recapture rate for hatchery smolts shows a similar drop-off with lateness of release. Nor is it likely that handling stress was responsible for the lower recapture rate recorded for the first migrants in the wild smolt run. Accordingly, the parabolic relationship between recapture rate and either tagging date for wild smolts or release date for hatchery smolts is presumed to reflect a real variation in survival rate over the four to six week period that smolts depart from a river (Pratt et al. 1975; Chadwick 1982).

The parabolic relationship between recapture rate for hatchery smolts and release time is also reported for smolts released into Swedish rivers (Larsson 1977a; Anon. 1983). Best survival rates for Swedish smolts were recorded when releases were made at the same time and temperature at which wild smolt runs occurred. The early to mid-May release period, which produced maximum recapture rates for hatchery smolts liberated into the LaHave River, is the time of the wild smolt migration (Hayes 1953).

Factors contributing to the parabolic relationships between survival rate and migration time for both wild and hatchery smolts might include forage availability or predator abundance, or both, in the estuary and nearby coastal waters. Both of these factors probably vary over the month or more post-smolts pass through these areas. Food in the estuary would be critical to the survival of young salmon since acclimation to sea water is particularly stressful to both hatchery and wild smolts (Bakshantansky et al. 1979, 1980) and metabolic rates would be high during this transition stage (Burrows 1969). The likelihood of food scarcity is heightened as a result of the seasonality of plankton blooms and the narrow size range in food items over which Atlantic salmon show a predatory response (Wankowski 1979). Predation probably increases during the course of the smolt run, as activity levels in all fish, including large predators, increase with rising estuarial temperatures. Food requirements of avian predators would also increase with lateness in the season as they forage for both themselves and their fledglings. Although consumption rates for predators probably increase from May through June, predation rates on smolts might not increase if appropriate buffer species were abundant.

Below average catches of small and large salmon in 1978 and 1979, respectively are assumed to represent reduced abundances of 1SW and 2SW salmon produced by smolts entering the sea in 1977.

Correspondingly reduced recapture rates for tagged hatchery smolts released into several rivers in Nova Scotia and New Brunswick (unpub. data) and low survival of smolts emigrating from Western Arm Brook in 1977 suggest that these reduced abundances were largely attributed to abnormally high natural mortality.

The broad distribution of populations from Maine to southern Labrador, whose 1977 smolts experienced below average survival, suggests that the additional mortality occurred outside the home river estuary and probably around Newfoundland, where populations from many North American rivers over winter (Templeman 1968; Reddin and Burfitt 1984). These losses would have occurred in the first sea-year since the 1977 smolts yielded below average productions of both 1SW and 2SW salmon. Post-smolts from southern rivers could have reached common northern feeding areas by mid-summer and maturing and non-maturing individuals from a single population would probably have remained together until after their first winter at sea (Reddin and Burfitt 1984; see section 2.0). The added mortality must therefore have occurred after mid-summer and before early spring.

The anomaly determined for the 1978 recreational catch of small salmon in Area N, Newfoundland (-47%), agrees with that indicated by a comparison of survival rates for smolts from the Western Arm Brook population of this same area. The survival of the 1977 smolt class of Western Arm Brook was 69% below the average survival rate for the four base-years (Fig. 5). Catch anomalies for other areas suggest that the 1977 smolts from many North American populations also experienced a reduction of 50% or more in survival.

Average or better catches of grilse were made in 1978 on upper Bay of Fundy rivers when below average catches were common to all other areas of Nova Scotia and New Brunswick. This is consistent with the difference in the sea distributions of these populations (see section 2.0). Difference in sea distribution might also have protected against higher natural mortality the other populations that showed no evidence of reduced return from the 1977 smolt class. Notable populations not seemingly affected are most of those along the eastern and southern coasts of insular Newfoundland.

Significant regressions between grilse returns to upper Bay of Fundy rivers and SST are not causal relationships, since sea temperatures in June-July would not have exceeded lethal limits. Rather, these relationships more probably reflect effects of temperature on forage conditions or predation, or both. The relationships determined for the two upper Bay of Fundy populations are consistent with those reported for pink salmon of the Fraser River (Vernon 1958), chinook salmon of the Columbia

River (Van Hyning 1973), and coho salmon from Oregon rivers (Scarnecchia 1981; Nichelson 1986).

Scarnecchia (1984a) related recreational catches of Atlantic salmon in northern Icelandic rivers to SST in June-July. A main difference between this relationship and that common to the other examples cited is that lower rather than higher sea temperatures were associated with depressed marine survival. Scarnecchia (1984a) observed fewer significant relationships between catches in southern Icelandic rivers and south coast sea temperatures, which were higher and varied less than north coast temperatures. The pattern common to all these relationships, including that reported for upper Bay of Fundy populations, is that sea temperature affects most the survival of those populations at the extremes of the species range.

Variation in predation probably explains the relationship between recruitment success of upper Bay of Fundy populations and sea temperature. The spiny dogfish (*Squalus acanthias*) is a major predator of fish and invertebrates (Bowman et al. 1984) that is often abundant in the Bay of Fundy during summer and fall (Annand 1985). Smolt classes experiencing higher sea temperatures might encounter more predators, including dogfish, if temperature influenced post-smolt or predator distribution. In section 2.3.3 it is shown that salmon distribution is influenced by sea temperature. In addition, reports of seasonal migrations to the north and south by dogfish (Templeman 1954; Colvocoresses and Musick 1980) suggest that temperature also influences the distribution of this potential predator.

About 50% of the variation in recruitment of grilse to two upper Bay of Fundy rivers was related to annual variation in sea temperature for June-July of the post-smolt year. A part of the remaining variation could be attributable to varying stock strength, which was not considered in regressions involving grilse catches for Stewiacke and Big Salmon rivers. Among the five years for which reliable smolt run estimates exist for Big Salmon River (Jessop 1975), annual smolt production varied by more than 100%.

The similarity of responses in recruitment for Big Salmon and Stewiacke populations to sea temperature support an earlier suggestion that these populations have similar sea distributions, which seem limited to the Bay of Fundy and nearby areas (see section 2.0).

The regressions between estimates of smolt-to-recruit survival for salmon of Western Arm Brook and the two different indices of winter sea temperatures in the northwest Atlantic indicate higher survival when warm SST extend far north during winter. One possible explanation is that salmon die because of

cold sea temperatures and that the extent of this mortality varies directly with the severity of winter conditions in the northwest Atlantic. Salmon encountering the lower lethal temperature of -0.7°C (Saunders et al. 1975) would probably die, particularly after extended exposure or if they came in contact with ice (Scholander et al. 1957). Prolonged exposure to cold sea temperatures has been noted to create an osmotic imbalance in Atlantic salmon and thereby cause their death (Bryne et al. 1972).

The relationship between survival and winter sea temperatures in the northwest Atlantic, although demonstrated only for post-smolts of Western Arm Brook, might also apply to other populations and sea ages which winter in this same general area. Tagging studies show that all North American salmon populations, except those of upper Bay of Fundy rivers, migrate to and from the northwest Atlantic (see section 2.0). Similarly, many European populations of salmon pass through the Labrador Sea to and from West Greenland coastal waters where they are generally abundant during late summer and fall (May 1973; Swain 1980; Reddin and Shearer 1987). Thus, recruitment of most North American and many European populations might be affected by winter temperature conditions in the northwest Atlantic.

The exceptionally low survival of the 1977 smolt class of Western Arm Brook may have been partly due to winter conditions in the northwest Atlantic. The two indices of sea temperature imply colder than average sea temperatures during the winter 1977-78 (Fig. 5). However, the predicted survival rates from both regressions were about twice that determined for the 1977 smolt class. These results suggest that cold winter conditions were not entirely, if at all, responsible for the widespread anomaly in survival recorded for the 1977 smolt class.

The varying winter temperature conditions in the northwest Atlantic may have affected the distribution of Western Arm Brook salmon (Reddin and Shearer 1987; section 2.0) and possibly that of its predators. However, these shifts should not have affected rate of predation markedly because the salmon would have been too large (Allen et al. 1972) for most predators, except very large fish and mammals.

The interpretation that recruitment within the Western Arm Brook population is adversely affected by cold sea temperatures should be viewed cautiously. Alternatively, winter temperatures would probably have affected distribution and thereby might have altered exploitation outside Area N. The estimates of survival assume that 20% of the annual commercial catch of 1SW salmon in Area N accounts for all the harvest outside the home river (i.e., both in and outside Area N) (Chadwick 1987). Following extremely cold winters in the northwest Atlantic, Western Arm

Brook salmon might commence their return migration from further south than they would following warmer winters. If salmon struck the east coast of Newfoundland further south, proportionately more of them might be caught before reaching Area N. Accordingly, both relationships for Western Arm Brook salmon may in part reflect variable exploitation outside Area N rather than recruitment variability solely.

Scale samples from 1SW salmon of the 1977 smolt class of the LaHave River showed no abnormal growth checks, although their rate of growth in summer-fall, determined from scales, was the lowest among the eleven smolt classes examined (Table 29). The low growth rate is assumed to reflect either poorer foraging conditions prevailing in the northwest Atlantic in 1977, or a shift in salmon distribution to the poorer foraging areas within this region. Either could have contributed to enhanced predation.

The reduced growth rate experienced by the 1977 smolt class should not have enhanced predation markedly considering that the average sea growth between smolt and 1SW salmon stages for the 1977 smolt class of LaHave salmon was within 2 cm of that determined for the 1978 and 1980 smolt classes. Similarly, the mean fork length of LaHave wild 1SW salmon from the 1977 smolt class was within 1 cm of an 8-year average (Cutting and Gray 1984). The mean lengths of 1SW salmon for the 1977 smolt class of Western Arm Brook (Chadwick 1987) and of the Miramichi River (Randall et al. 1985b) were also within 1 cm of 13 year averages for these respective populations, which as well showed below average recruitment from the 1977 smolts (Table 25; Fig. 5).

The recovery of salmon tags in two different rookeries, from releases in four different rivers and in several years suggest that cormorants commonly prey on tagged hatchery smolts. Meister (1969) reported predation by double-crested cormorants on externally tagged hatchery smolts released into the Machias River, Maine, USA, in 1966 and 1967. It is unlikely that the external tags attracted the predator since the tags were relatively small (15 mm X 5 mm), generally dark in colour (blue or green) and not known to seriously affect mobility (Eisner and Ritter 1979). Predation of salmon without externally visible tags has been confirmed recently from stomach contents of birds collected in May and June 1987, along four rivers on Nova Scotia's eastern shore, i.e., St. Mary's, Liscomb and East and West rivers, Sheet Harbour (G. J. Farmer, Department of Fisheries and Oceans, Halifax, Nova Scotia, pers. comm.). In this recent study untagged smolts of both wild and hatchery origin were found.

The tags recovered from the two rookeries along the Nova Scotia coast clearly do not represent total losses of hatchery

smolts to cormorant predation. The low numbers of tags from other than the current year probably represents reduced efficiency of retrieval with the elapsed time between deposit and search. This is probably the reason for the absence of tags from releases prior to 1981, despite more than 200,000 tagged hatchery smolts having been released into rivers near the two rookeries (i.e., LaHave, Medway and Liscomb rivers) from 1971 to 1980 (unpub. data).

Tags from the cormorant rookery on Tobacco Island suggest that more of the earlier released smolts were consumed by cormorants. The later release date, May 26, probably coincides more closely with the run of the wild smolts from the St. Mary's River which, if similar to those reported for East and West rivers, Sheet Harbour (Ducharme 1972), should peak in late May or early June. This implied change in predation rate with migration time, is consistent with relationships between tag recapture rate and either wild smolt migration time on the Miramichi River or hatchery smolt release time in the LaHave River. Lower recapture rates for early migrants or releases probably reflect greater losses to predation.

The cormorant predation on salmon reported herein pertains to hatchery smolts. Whether those consumed were healthy fish or had impaired mobility is unknown. The 1987 follow-up study showed that wild smolts are consumed by cormorants (G. J. Farmer, pers. comm.), although relative predation on wild and hatchery smolts in these rivers remains unknown. A recent study on the Bush River, Northern Ireland, found heavy predation on wild smolts (50% or more of the total run) by the great cormorant (*P. carbo*) and an apparent preference for hatchery smolts (Kennedy and Greer 1988). Although this apparent selectivity is based on the stomach contents of only four birds, it is consistent with general perceptions that wild smolts are less vulnerable to predators than hatchery smolts (Anon. 1983; Larsson 1985). Wild smolts would be more wary (Ginetz and Larkin 1976) and more dispersed during migration than hatchery smolts (Anon. 1983). Wild smolts of the St. Mary's population might also have been predated upon less by cormorants in 1986 than the hatchery smolts, particularly if they migrated later, as is suspected.

Reports that salmonids are rarely found in stomach samples or regurgitations from double-crested cormorants (Milton and Austin-Smith 1983a) do not prove that cormorants have negligible effect on salmonids, since sampling programs have not been extensive in time or space. Public concern about predation on salmonids is prompted by increases in cormorants in many coastal areas of the Maritime provinces. In Nova Scotia these increases have been perhaps as much as 10 and 4% per year for double-crested and great cormorants since at least the early 1970s (Milton and Austin-Smith 1983b).

There is no evident overall decline in recruitment since the mid-1970s as would be expected if post-smolt survival varied inversely with apparent increases in cod. However, Larsson (1980) reported that salmon were in 65% of cod stomachs collected off the mouth of a Swedish west coast river during the smolt run, and Hvidsten and Møkkelgjerd (1987) reported heavy predation of tagged post-smolts by cod in the estuary of the River Surna, Norway. The impact of cod on post-smolt survival is probably localized to specific estuaries and coastal areas. The current analysis was presumed to be sensitive to a major increase in cod predation over a broad geographic range. It would not have detected localized changes that may have occurred. The double-crested cormorant is also a predator whose effect would be localized considering that it is concentrated about breeding colonies which are unevenly distributed and generally in or near specific river estuaries (Milton and Austin-Smith 1983a, 1983b).

The absence of a long-term trend in recruitment indices also suggests that grey seals do not add much to the total natural mortality experienced by a smolt class. Although more specific studies indicate that grey seals consume salmon that are generally larger than 1.0 kg, the authors of these studies have also indicated their suspicions that perhaps most of the salmon consumed are pilfered from commercial fishing gear (Rae 1968; Mansfield and Beck 1977; Anon. 1983). With respect to North American salmon there is no evidence that grey seals capture and kill large numbers of free-swimming individuals.

Different predation rates might explain why smolt-to-recruit survival rates for salmon of the Big Salmon River are less than half those for the Sand Hill River population. Salmon from Big Salmon spend their entire sea life in and near the Bay of Fundy (see section 2.0) whereas those from Sand Hill are assumed to occupy the area immediately east and north of insular Newfoundland (Pratt et al. 1974). If salmon of Big Salmon suffer greater predation than those from more northern rivers, we might expect other southern populations, including those that migrate through southern waters to and from the northern feeding areas, to experience higher losses to predation. Predators of salmon are probably more abundant toward the southern end of the breeding range and their consumption rates would be greater because of higher sea temperatures (Pauly 1979).

3.5 CONCLUSIONS

Smolt-to-recruit survival varies among populations of North American salmon and annually. Average survival rates of less than 10% determined for Big Salmon River smolts and more than 20% for Sand Hill River smolts probably represent the range in average survival for North American populations. Difference

between average survival rates for these two populations is believed to be attributed to different predation rates and to reflect a tendency for southern populations to experience greater natural mortality as post-smolts. Within populations annual marine survival can be depressed as much as 50% or more as observed for the 1977 smolt class of many North American populations and also evident among estimates for five smolt classes of the Big Salmon River.

Natural mortality rates for post-smolts and previous spawners of Big Salmon River are higher and lower, respectively, than corresponding rates for non-upper Bay of Fundy populations. In the life history strategy for upper Bay of Fundy populations, the lower mortality between spawnings compensates for the higher post-smolt mortality.

Rate of natural mortality continues to be variable late in the sea-life of the salmon as indicated by both the relationships between smolt-to-recruit survival and winter SST in the Labrador Sea and the identification of late-summer or later as the period that the 1977 smolt class experienced above average natural mortality.

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Table 1a. Location and time of recovery as post-smolts from tagged wild and native hatchery smolts emigrating from Big Salmon River, New Brunswick, 1967 to 1973.

Recovery location		Month of recovery							Total
NAFO	Description	May	June	July	Aug.	Sep.	Oct.	UNK.	tags
	New Brunswick								
4X	Lower Fundy	-	1	2	30	4	-	1	38
	Nova Scotia								
4X	Lower Fundy	-	-	5	20	-	-	2	27

Table 1b. Location and time of recovery as post-smolts from tagged hatchery smolts emigrating from Lower Fundy and Gulf of Maine rivers. Lower Fundy river smolts were native hatchery smolts released into the Saint John River, New Brunswick, 1967 to 1984. Recaptures for Maine smolts, released from 1966 and 1983, were reported by Meister (1984).

Recovery location		Home river	Month of recovery							Total tags
NAFO	Description		May	June	July	Aug.	Sep.	Oct.	UNK.	

River Mouth										
5Y		Maine	2	-	-	-	-	-	-	2
4X		Saint John	4	-	-	-	-	-	-	4
New Brunswick										
4X	Lower Fundy	Maine	-	-	-	11	2	-	-	13
		Saint John	-	1	1	1	-	-	-	3
Nova Scotia										
4X	Lower Fundy	Maine	-	-	49	67	2	-	2	120
		Saint John	-	2	17	5	1	-	-	25
4X	Southwest Shore	Maine	-	16	66	3	-	1	-	86
		Saint John	-	7	5	-	-	-	2	14
4W	Eastern Shore	Maine	-	14	6	-	-	-	-	20
		Saint John	-	4	-	-	-	-	-	4
4Vn	Cape Breton East	Maine	-	1	1	-	-	-	-	2
		Saint John	-	-	-	-	-	-	-	-
Newfoundland										
3Pn	Area J	Maine	-	2	7	-	-	-	-	9
+3Ps		Saint John	-	-	-	-	-	-	-	-
3Ps	Area I	Maine	-	1	3	-	-	-	-	4
		Saint John	-	-	1	1	-	-	-	2
3L	Area C	Maine	-	-	-	1	-	-	-	1
		Saint John	-	-	-	-	-	-	-	-
3K	Area B	Maine	-	-	-	1	1	-	-	2
		Saint John	-	-	-	1	-	-	-	1
4R	Area N	Maine	-	-	-	-	-	-	-	-
		Saint John	-	-	2	-	-	-	-	2
Labrador										
4R	Southern	Maine	-	-	1	-	-	-	-	1
+2J		Saint John	-	-	-	-	1	-	-	1

Table 1c. Location and time of recovery as post-smolts from tagged hatchery smolts emigrating from rivers in southwest Nova Scotia, 1971 to 1984. Smolts were progeny of salmon from Medway and LaHave rivers.

Recovery location		Home river	Month of recovery							Total tags
NAFO	Description		May	June	July	Aug.	Sep.	Oct.	UNK.	
River Mouth										
4X		LaHave	5	36	3	-	-	-	-	44
		Medway	2	3	-	-	-	-	-	5
		Mersey	-	-	-	-	-	-	-	-
Nova Scotia										
4X	Southwest Shore	LaHave	-	2	-	-	-	-	-	2
		Medway	-	3	6	-	-	-	-	9
		Mersey	-	-	-	-	1	-	-	1
4X	Lower Fundy	LaHave	-	-	1	-	-	-	-	1
		Medway	-	-	-	1	-	-	-	1
		Mersey	-	-	-	-	-	-	-	-
4W	Eastern Shore	LaHave	-	11	-	-	-	-	-	11
		Medway	-	1	-	-	-	-	-	1
		Mersey	-	-	-	-	-	-	-	-
4Vn	Cape Breton	LaHave	-	-	-	-	-	-	-	-
		Medway	-	1	-	-	-	-	-	1
		Mersey	-	-	-	-	-	-	-	-
Newfoundland										
3Pn	Area J	LaHave	-	-	1	-	-	-	-	1
+3Ps		Medway	-	-	-	-	-	-	-	-
		Mersey	-	-	-	-	-	-	-	-
3Ps	Area I	LaHave	-	-	1	-	-	-	-	1
		Medway	-	-	-	-	-	-	-	-
		Mersey	-	-	1	-	-	-	-	1
3K	Area A	LaHave	-	-	-	-	-	-	-	-
		Medway	-	-	1	-	-	-	-	1
		Mersey	-	-	-	-	-	-	-	-
Quebec										
4S	Lower North Shore	LaHave	-	-	2	-	-	-	-	2
		Medway	-	-	-	-	-	-	-	-
		Mersey	-	-	-	-	-	-	-	-
Labrador										
2J	Northern	LaHave	-	-	-	-	-	-	-	-
		Medway	-	-	-	-	-	-	-	-
		Mersey	-	-	-	1	1	-	-	2

Table 1d. Location and time of recovery as post-smolts from tagged wild and hatchery smolts emigrating 1959 to 1982, from rivers emptying into the Gulf of St. Lawrence, i.e., Margaree River and River Philip, Nova Scotia, Miramichi River, New Brunswick, and several Quebec rivers grouped according to geographic areas of the Gaspé, Anticosti Island and Upper North Shore. Recaptures from Quebec smolts were reported by Caron (1983).

Recovery location		Home river ¹	Month of recovery							Total tags
NAFO	Description		May	June	July	Aug.	Sep.	Oct.	UNK.	

River Mouth										
4T		Margaree	-	-	-	-	-	-	-	-
+4S		R. Philip	-	-	-	-	-	-	-	-
		Miramichi	1	12	-	-	-	-	-	13
		Gaspe	-	-	-	-	-	-	-	-
		Anticosti	-	-	-	-	-	-	-	-
		Upper North Shore	1	5	1	1	-	-	-	8
New Brunswick										
4T	Gulf Shore	Margaree	-	-	-	-	-	-	-	-
		R. Philip	-	1	-	-	-	-	-	1
		Miramichi	-	-	-	1	-	-	-	1
		Gaspe	-	-	-	-	-	-	-	-
		Anticosti	-	-	-	-	-	-	-	-
		Upper North Shore	-	-	-	-	-	-	-	-
Prince Edward Island										
4T	North Shore	Margaree	-	-	-	-	-	-	-	-
		R. Philip	-	1	-	-	-	-	-	1
		Miramichi	-	-	-	-	-	-	-	-
		Gaspe	-	-	-	-	-	-	-	-
		Anticosti	-	-	-	-	-	-	-	-
		Upper North Shore	-	-	-	-	-	-	-	-
Quebec										
4T	Gaspe	Margaree	-	-	-	-	-	-	-	-
		R. Philip	-	-	-	-	-	-	-	-
		Miramichi	-	-	-	-	1	1	-	2
		Gaspe	-	-	-	-	-	-	-	-
		Anticosti	-	-	-	-	-	-	-	-
		Upper North Shore	-	-	-	-	-	-	-	-

4S	Upper North Shore	Margaree	-	-	-	-	-	-	-
		R. Philip	-	-	-	-	-	-	-
		Miramichi	-	-	-	-	-	-	-
		Gaspe	-	-	-	-	-	-	-
		Anticosti	-	-	-	-	-	-	-
		Upper North Shore	-	-	-	-	1	-	1
4S	Lower North Shore	Margaree	-	-	-	-	-	-	-
		R. Philip	-	-	-	-	-	-	-
		Miramichi	-	-	-	1	-	-	1
		Gaspe	-	-	1	-	-	-	1
		Anticosti	-	-	-	1	-	-	1
		Upper North Shore	-	-	-	-	-	-	-
4R +2J	Labrador Southern	Margaree	-	-	-	-	1	-	1
		R. Philip	-	-	-	-	-	-	-
		Miramichi	-	-	-	1	-	-	1
		Gaspe	-	-	-	-	-	-	-
		Anticosti	-	-	-	-	-	-	-
		Upper North Shore	-	-	-	-	1	-	1
4R	Newfoundland Area N	Margaree	-	-	-	-	-	-	-
		R. Philip	-	-	-	-	-	-	-
		Miramichi	-	-	-	-	-	-	-
		Gaspe	-	-	2	-	-	-	2
		Anticosti	-	-	-	-	-	-	-
		Upper North Shore	-	-	-	-	-	-	-
3K	Area A	Margaree	-	-	-	-	-	-	-
		R. Philip	-	-	-	-	-	-	-
		Miramichi	-	-	1	-	-	-	1
		Gaspe	-	-	-	-	-	-	-
		Anticosti	-	-	-	-	-	-	-
		Upper North Shore	-	-	-	-	-	-	-
3L	Area F	Margaree	-	-	-	-	-	-	-
		R. Philip	-	-	-	-	-	-	-
		Miramichi	-	-	-	-	-	-	-
		Gaspe	-	-	1 ²	-	-	-	1
		Anticosti	-	-	-	-	-	-	-
		Upper North Shore	-	-	-	-	-	-	-
4Vn	Nova Scotia Cape Breton East	Margaree	-	1	-	-	-	1	2
		R. Philip	-	-	-	-	-	-	-

	Miramichi	-	-	-	-	-	-	-
	Gaspé	-	1	-	-	-	-	1
	Anticosti	-	-	-	-	-	-	-
	Upper North Shore	-	-	-	-	-	-	-
4X Lower Fundy	Margaree	-	-	-	-	-	-	-
	R. Philip	-	-	-	-	-	-	-
	Miramichi	-	-	-	1	-	-	1
	Gaspé	-	-	-	-	-	-	-
	Anticosti	-	-	-	-	-	-	-
	Upper North Shore	-	-	-	-	-	-	-

¹Designates home river or geographic area in which home river is located.

²Recaptured in either June or July (Caron 1983).

Table 2a. Location and time of recovery as 1SW and 2SW salmon at mouth of home river and in the sea from tagged wild and native hatchery smolts emigrating from Big Salmon River, 1967 to 1973.

Recovery location		Sea age	Month of recovery								Total tags
NAFO	Description		May	June	July	Aug.	Sep.	Oct.	Nov.	UNK.	
River ¹											
4X		1	-	1	11	25	31	4	-	-	72
		2	-	-	-	-	1	-	-	-	1
New Brunswick											
4X	Middle Fundy	1	-	-	-	1	1	-	-	-	2
		2	-	-	3	-	-	-	-	-	3
Nova Scotia											
4X	Lower Fundy	1	-	-	-	-	-	-	-	-	-
		2	-	-	-	1	-	-	-	-	1
Nova Scotia											
4X	Lower Fundy	1	-	-	-	1	1	-	-	-	2
		2	-	1	-	-	-	-	-	-	1
Newfoundland											
3Pn	Area J ₂	1	-	-	-	-	-	-	-	-	-
+3Ps		2	-	1	-	-	-	-	-	-	1

¹ Recoveries at counting fence situated less than 200 m upstream of head of tide.

Table 2b. Location and time of recovery as 1SW and 2SW salmon at mouth of home river and in the sea from tagged native hatchery smolts released into the Saint John River, 1967 to 1984.

[illegible]

Table 2c. Location and time of recovery as 1SW and 2SW salmon at the mouth of home river and in the sea from tagged hatchery smolts released into the LaHave River, 1971 to 1984. Smolts originated from salmon returning to Medway and LaHave rivers.

Recovery location		Sea age	Month of recovery								Total tags
NAFO	Description		May	June	July	Aug.	Sep.	Oct.	Nov.	UNK.	

River Mouth											
4X		1	-	56	39	2	-	-	-	5	102
		2	20	33	3	-	-	-	-	8	64
Nova Scotia											
4X	Southwest Shore	1	-	12	-	-	-	-	-	-	12
		2	1	1	-	-	-	-	-	-	2
4X	Lower Fundy	1	-	-	2	-	-	-	-	-	2
		2	-	1	1	-	-	-	-	-	2
4W	Eastern Shore	1	-	3	8	4	1	-	-	1	17
		2	1	5	2	-	-	-	-	-	8
4Vn +4W	Cape Breton East	1	-	22	12	-	-	-	-	-	34
		2	-	1	-	-	-	-	-	-	1
4T	Gulf Shore	1	-	-	2	-	-	-	-	-	2
		2	-	-	-	-	-	-	-	-	-
Quebec											
4T	Gaspé	1	-	-	-	-	1	-	-	-	1
		2	-	-	-	-	-	-	-	-	-
Newfoundland											
4R	Area K	1	-	1	2	-	-	-	-	-	3
		2	-	-	-	-	-	-	-	-	-
3Pn +3Ps	Area J	1	-	3	3	-	-	-	-	-	6
		2	1	-	-	-	-	-	-	-	1
3Ps	Area I	1	-	-	1	-	-	-	-	-	1
		2	-	-	-	-	-	-	-	-	-
3Ps	Area H	1	-	2	5	-	-	-	-	-	7
		2	-	-	-	-	-	-	-	-	-
3Ps	Area F	1	2	11	3	-	-	-	-	2	18
		2	1	-	-	-	-	-	-	-	1
3L	Area E	1	1	7	3	-	-	-	-	-	11

Table 2d. Location and time of recovery as 1SW and 2SW salmon at mouth of home river and in the sea from tagged wild smolts emigrating from the Miramichi River, 1968 to 1976.

Recovery location		Sea age	Month of recovery								Total tags
NAFO	Description		May	June	July	Aug.	Sep.	Oct.	Nov.	UNK.	
River Mouth											
4T		1	-	5	11	4	3	1	-	-	24
		2	1	47	21	5	3	2	-	-	79
New Brunswick											
4T	Gulf Shore	1	-	-	2	1	2	-	-	-	5
		2	-	-	4	-	-	-	-	-	4
Quebec											
4T	Gaspé	1	-	-	1	-	-	-	-	-	1
		2	-	1	2	-	-	-	-	-	3
4S	Lower North Shore	1	-	-	1	-	-	-	-	-	1
		2	-	-	-	-	-	-	-	-	-
Prince Edward Island											
4T	North Shore	1	-	-	-	-	-	-	-	-	-
		2	-	-	2	-	-	-	-	1	3
Nova Scotia											
4Vn	Cape Breton	1	-	-	-	-	-	-	-	-	-
+4W	East	2	-	2	-	-	-	-	-	-	2
4W	Southwest Shore	1	-	1	2	-	-	-	-	-	3
		2	-	-	1	-	-	-	-	-	1
4X	Lower Fundy	1	-	-	1	-	-	-	-	-	1
		2	-	-	-	1	-	-	-	1	2
Newfoundland											
4R	Area K	1	-	-	-	-	-	-	-	-	-
		2	-	3	-	-	-	-	-	-	3
3Pn	Area J	1	-	5	6	-	-	-	-	-	11
+3Ps		2	9	26	3	-	-	-	-	-	38
3Ps	Area I	1	-	4	4	-	-	-	-	-	8
		2	1	3	1	1	-	-	-	-	6
3Ps	Area H	1	-	7	11	-	-	-	-	-	18
		2	4	4	2	-	-	-	-	-	10

3Ps	Area G	1	-	-	3	-	-	-	-	-	3
		2	-	-	-	-	-	-	-	-	-
3L	Area F	1	-	8	-	1	-	-	-	-	9
		2	7	9	-	-	-	-	-	-	16
3L	Area E	1	-	7	8	-	-	-	-	-	15
		2	5	8	-	-	-	-	-	-	13
3L	Area D	1	-	9	16	2	-	-	-	1	28
		2	8	13	1	-	-	-	-	-	22
3L	Area C	1	-	11	15	1	1	-	-	-	28
		2	8	23	2	-	2	-	-	1	36
3K	Area B	1	-	12	14	-	-	-	-	-	26
		2	1	14	2	1	-	-	-	-	18
3K	Area A	1	-	24	53	10	-	-	-	4	91
		2	-	11	7	1	-	-	-	2	21
4R	Area N	1	-	-	1	-	-	-	-	-	1
		2	-	-	-	-	-	-	-	-	-
4R	Area M	1	-	-	-	1	-	-	-	-	1
		2	-	-	-	-	-	-	-	-	-
4R +2J	Labrador Southern	1	-	-	3	1	-	-	-	1	5
		2	-	-	1	-	-	-	-	1	2
1F	Greenland	1	-	-	1	7	7	6	1	-	24
		2	-	-	-	-	-	-	-	-	-
1E		1	-	-	-	8	8	7	-	1	24
		2	-	-	-	1	-	-	-	-	1
1D		1	-	-	1	13	9	7	-	-	30
		2	-	-	-	-	-	1	-	-	1
1C		1	-	-	3	18	12	6	-	4	43
		2	-	-	2	-	-	-	-	-	2
1B		1	-	-	-	2	11	5	-	9	27
		2	-	-	-	-	-	-	-	1	1
1A		1	-	-	-	1	6	4	2	2	15
		2	-	-	-	1	-	1	-	-	2
1	Unknown	1	-	-	-	10	14	25	5	26	80
		2	-	-	-	-	1	1	-	-	2

Table 3a. Location and time of recovery as previous spawners at mouth of home river and in the sea for maturing salmon of Saint John River, tagged in river during preceding spawning migrations, 1967 to 1983. Recaptures in river and in year of tagging are excluded.

Recovery location		Year of recapture	Month of recovery								Total tags
NAFO	Description		May	June	July	Aug.	Sep.	Oct.	Nov.	UNK.	
River Mouth											
4X		1	10	5	32	8	1	-	-	-	56
		2	-	5	7	1	-	-	-	-	13
New Brunswick											
4X	Lower Fundy	1	-	-	-	-	-	1	-	1	2
		2	-	-	-	-	-	-	-	-	-
Nova Scotia											
4X	Lower Fundy	1	-	4	2	1	-	-	-	1	8
		2	-	-	-	-	-	-	-	-	-
4X	Southwest Shore	1	-	2	7	-	-	-	-	-	9
		2	-	-	-	-	-	-	-	-	-
4W	Eastern Shore	1	-	-	6	-	-	-	-	-	6
		2	-	-	-	-	-	-	-	-	-
4T	Gulf Shore	1	-	-	-	-	-	-	-	-	-
		2	-	1	1	-	-	-	-	-	2
Newfoundland											
4R	Area K	1	-	-	1	-	-	-	-	-	1
		2	-	-	-	-	-	-	-	-	-
3Pn +3Ps	Area J	1	-	8	5	-	-	-	-	-	13
		2	-	-	-	-	-	-	-	-	-
3Ps	Area I	1	-	5	23	1	-	-	-	-	29
		2	-	2	-	-	-	-	-	-	2
3Ps	Area H	1	-	3	18	-	-	-	-	2	23
		2	-	-	-	-	-	-	-	-	-
3L	Area G	1	-	-	12	-	-	-	-	2	14
		2	-	-	-	-	-	-	-	-	-
3L	Area F	1	-	1	5	-	-	-	-	-	6
		2	-	-	-	-	-	-	-	-	-
3L	Area E	1	-	-	2	-	-	-	-	-	2

Table 3b. Location and time of recovery as previous spawners at mouth of home river and in the sea for maturing salmon of Miramichi River, tagged in river during preceding spawning migrations, 1967 to 1983. Recaptures in river and in year of tagging are excluded.

Recovery location		Year of recapture	Month of recovery								Total tags
NAFO	Description		May	June	July	Aug.	Sep.	Oct.	Nov.	UNK.	
River Mouth											
4T		1	1	2	3	3	-	-	-	-	9
		2	2	2	8	2	-	-	-	-	14
Quebec											
4T	Gaspé	1	-	1	1	-	-	-	-	-	2
		2	-	-	-	-	-	-	-	-	-
Lower North											
4S	Shore	1	-	-	14	2	-	-	-	-	16
		2	-	-	-	-	-	-	-	-	-
Prince Edward Island											
4T	North Shore	1	-	1	1	-	-	-	-	-	2
		2	-	-	-	-	-	-	-	-	-
Nova Scotia											
4T	Gulf Shore	1	-	-	1	-	-	-	-	-	1
		2	-	-	-	-	-	-	-	-	-
Newfoundland											
3Pn +3Ps	Area J	1	-	-	-	-	-	-	-	-	-
		2	1	6	-	-	-	-	-	-	7
3Ps	Area H	1	-	1	-	-	-	-	-	-	1
		2	1	1	-	-	-	-	-	-	2
3L	Area F	1	-	-	-	-	-	-	-	-	-
		2	1	1	-	-	-	-	-	-	2
3L	Area E	1	-	-	-	-	-	-	-	-	-
		2	2	1	-	-	-	-	-	-	3
3L	Area D	1	-	-	-	-	-	-	-	-	-
		2	3	5	-	-	-	-	-	-	8
3L	Area C	1	-	-	1	-	-	-	-	-	1
		2	-	2	-	-	-	-	-	1	3
3K	Area B	1	-	-	-	-	-	-	-	-	-
		2	-	2	-	-	-	-	-	-	2

3K	Area A	1	2	15	1	-	-	-	-	1	19
		2	-	-	-	-	-	-	-	-	-
4R	Area N	1	-	3	3	2	-	-	-	-	8
		2	-	-	-	-	-	-	-	-	-
4R	Area M	1	-	-	4	-	-	-	-	-	4
		2	-	-	-	-	-	-	-	-	-
4R	Area L	1	-	1	-	-	-	-	-	-	1
		2	-	-	-	-	-	-	-	-	-
Labrador											
4R	Southern	1	-	1	8 ¹	4 ¹	-	1	-	1	15
+2J		2	-	-	2 ¹	1 ¹	-	-	-	-	3
2J	Northern	1	-	-	1	-	-	-	-	-	1
+2H		2	-	-	-	-	-	-	-	-	-
+2G											
Greenland											
1F		1	-	-	-	1	-	-	-	-	1
		2	-	-	-	-	-	-	-	-	-
1E		1	-	-	-	2	-	-	-	-	2
		2	-	-	-	-	-	-	-	-	-
1D		1	-	-	-	1	2	-	-	-	3
		2	-	-	-	-	-	-	-	-	-
1C		1	-	-	-	1	1	1	-	-	3
		2	-	-	-	-	-	-	-	-	-
1B		1	-	-	-	-	1	-	2	-	3
		2	-	-	-	-	-	-	-	-	-
1A		1	-	-	-	-	1	-	-	1	2
		2	-	-	-	-	-	-	-	-	-
1	Unknown	1	-	-	-	2	1	-	-	-	3
		2	-	-	-	-	-	-	-	-	-

¹ Anomaly to normal migration pattern unless salmon either destined to remain at sea an extra year before spawning or spawned in year 1.

Table 4. Annual variation in northward distributions of commercial catches of small (<2.7 kg) and large (≥2.7 kg) salmon along east and south coasts of insular Newfoundland, 1969 to 1984. Northward distribution is expressed as the proportion of catch in Areas A to I, caught in Areas A and B. Catch data are from O'Connell et al. (1985).

Fishery year	Small Salmon			Large Salmon		
	Areas	Areas A + B		Areas	Areas A + B	
	A to I	Number	Prop'n	A to I	Number	Prop'n
1969	175790	83924	.48	59253	28681	.49
1970	253524	129573	.51	77460	35969	.47
1971	133964	71002	.53	107489	58757	.55
1972	155295	54197	.35	70809	39190	.55
1973	255229	121738	.48	124567	45972	.37
1974	216900	60329	.28	106154	30019	.28
1975	227885	131528	.58	123535	49984	.40
1976	177512	119549	.67	98284	55001	.56
1977	175888	106342	.60	131886	71765	.54
1978	86909	43552	.50	77493	32239	.42
1979	163342	124604	.76	37390	23111	.62
1980	228397	144107	.63	110508	58882	.53
1981	197044	138104	.70	112736	63111	.56
1982	181070	110192	.61	56181	33362	.59
1983	134343	93281	.69	56467	33546	.59
1984	122234	64017	.52	47383	25731	.54

Table 5a. Annual variation in the northward distributions of recaptures from tagged wild smolts of Miramichi River recovered as 1SW and 2SW salmon along east and south coasts of insular Newfoundland. Northward distribution is expressed as the proportion of recaptures in Areas A to I, recovered in Areas A and B.

Recapture year	1SW salmon			2SW salmon		
	Areas	Areas A + B		Areas	Areas A + B	
	A to I	Number	Prop'n	A to I	Number	Prop'n
1969	8	6	.75	-	-	
1970	30	19	.63	5	0	.00
1971	28	19	.68	33	12	.36
1972	15	5	.33	2	0	.00
1973	16	14	.88	10	3	.30
1974	26	7	.27	4	0	.00
1975	51	18	.35	20	2	.10
1976	17	11	.65	42	13	.31
1977	34	17	.50	12	6	.50
1978	-	-	-	14	2	.14

Table 5b. Annual variation in the northward distributions of recaptures from tagged hatchery smolts of Saint John and LaHave rivers recovered as 1SW salmon along east and south coasts of insular Newfoundland. Northward distribution is defined as the proportion of recaptures in Areas A to I, recovered in Areas A and B.

Recapture year	Saint John			LaHave		
	Areas A to I	Areas A + B		Areas A to I	Areas A + B	
		Number	Prop'n		Number	Prop'n
1970	7	5	.71	-	-	-
1971	1	1	1.00	-	-	-
1972	3	0	0.00	-	-	-
1973	3	1	.33	10	1	.10
1974	26	3	.12	14	0	.00
1975	40	6	.15	19	3	.16
1976	20	9	.45	-	-	-
1977	39	23	.59	24	12	.50
1978	21	16	.76	-	-	-
1979	17	10	.59	19	9	.47
1980	59	52	.88	3	1	.33
1981	5	2	.40	15	11	.73
1982	7	2	.29	-	-	-
1983	7	6	.86	-	-	-
1984	9	4	.44	-	-	-

Table 6. Results of variance test for homogeneity of proportions of salmon catches and tag recaptures along east and south coasts of insular Newfoundland made in northern Areas A and B.

Catch/tag recapture series	Degrees of freedom	Chi-square	Prob.
catch, small salmon	15	184055.	<0.001
catch, large salmon	15	47886.	<0.001
Miramichi, 1SW salmon	8	29.60	<0.001
Miramichi, 2SW salmon	8	13.29	0.103
Saint John, 1SW salmon	14	87.19	<0.001
LaHave, 1SW salmon	6	26.50	<0.001

Table 7. Numbers and proportions of tag recaptures as 1SW salmon in Newfoundland-Labrador fishery and at Greenland from native hatchery smolts released into Saint John River.

Fishery year	Recaptures (maturing 1SW salmon excluded)				
	Total ¹ number	Nfld-Lab Number	1SW Prop'n	Greenland Number	1SW Prop'n
1970	30	7	.23	3.0 ²	.10
1971	28	2	.07	6.0 ²	.21
1972	139	4	.03	9.5 ²	.07
1973	51	3	.06	8.0 ²	.16
1974	284	35	.12	46.5 ²	.16
1975	111	28	.25	11.5 ²	.10
1976	230	29	.13	41.0	.18
1977	189	55	.29	7.0	.04
1978	172	28	.16	23.0	.13
1979	424	26	.06	84.0	.20
1980	373	73	.20	31.0	.08
1981	142	11	.08	23.0	.16
1982	68	10	.15	13.0	.19
1983	65 ³	10	.15	1.0	.02
1984	48 ³	6	.13	3.0	.06

¹Total recaptures as non-maturing 1SW salmon and MSW salmon in sea fisheries and home river.

²Number of recaptures previously halved to compensate for greater fishing effort. See text for explanation.

³Includes 9 unreported 2SW salmon estimated to have been recaptured in an Indian fishery in home river. Estimate based on an assumed exploitation for this fishery equal to the mean of rates derived for MSW salmon in years 1978 to 1982 (Marshall 1985).

Table 8. Index of spring SST along the east coast of Newfoundland, 1969 to 1984. Measurements are Julian days when the 0°C isotherm in coastal waters off eastern Newfoundland receded north of 50°N .

Year	0°C isotherm recession date	
	Calendar	Julian
1969	May 9	129
1970	Jun 5	156
1971	May 21	141
1972	Jun 23	175
1973	Jun 1	152
1974	Jul 6	187
1975	Jun 26	177
1976	May 13	134
1977	May 19	139
1978	May 25	145
1979	May 24	144
1980	May 1	122
1981	Apr 30	120
1982	May 15	135
1983	May 10	130
1984	Jun 10	162

Table 9. Regression coefficients and their significance for linear comparisons of proportions of salmon caught or recaptured in Areas A and B, Newfoundland, on Julian day that 0°C isotherm receded north of 50°N .

Dependent variable	Degrees of freedom ¹	Regression		
		Coeff.	St. Error	Prob.
catch, small salmon	14	-0.0176	0.0049	0.003
catch, large salmon	14	-0.0124	0.0037	0.005
Miramichi, 1SW salmon	7	-0.0285	0.0088	0.014
Miramichi, 2SW salmon	7	-0.0315	0.0115	0.028
Saint John, 1SW salmon	13	-0.0480	0.0098	<0.001
LaHave, 1SW salmon	5	-0.0445	0.0114	0.010

¹Degrees of freedom in residual mean square.

Table 10. Indices of SST in Labrador Sea and along west coast of Greenland, 1970 to 1984. Data are from Reddin and Shearer (1987).

Year	Latitude ($^{\circ}$ N) of 4° C isotherm west of 45° W		Area (1000 km^2) of 4° C or warmer water north of 50° N and west of 40° W	Extent (%) of Greenland coast covered by 4° C isotherm
	January (VAR1)	August (VAR 2)	January (VAR3)	August (VAR4)
1970	59.0	68.5	73	5
1971	61.5	72.5	102	60
1972	51.0	71.5	19	40
1973	58.0	68.5	83	50
1974	58.0	74.5	59	80
1975	57.0	74.5	49	25
1976	56.5	71.5	54	65
1977	58.0	74.5	64	80
1978	52.0	70.0	37	60
1979	60.5	72.5	88	100
1980	55.5	75.0	41	100
1981	52.0	75.0	45	40
1982	55.5	75.0	46	15
1983	55.0	66.0	45	0
1984	47.0	64.0	20	0

Table 11. Numbers of virgin salmon, categorized by sea age, returning to Big Salmon River, 1967 to 1973. Numbers derived from fence counts and angling catch estimates partitioned on the basis of fork length into grilse (<63.5 cm) and large salmon (≥63.5 cm) and aging data reported for representative samples of fish trapped at counting fence.

Year	Returns to counting fence						Returns to river				
	All fish ¹		Aged Fish ²				All fish ⁴		Virgin fish ⁵		
	Grilse	Total	1SW	2SW	3SW	PS ³	Grilse	Total	1SW	2SW	3SW
1	2	3	4	5	6	7	8	9	10	11	12
1967	779	2505	34	27	0	106	1465	4089	959	635	0
1968	1243	2531	439	53	10	425	1324	2703	1271	155	29
1969	188	1274	14	34	0	311	423	1630	112	145	0
1970	430	1308	255	9	0	361	592	1605	735	21	0
1971	374	678	196	2	0	120	510	872	570	5	0
1972	933	1360	379	4	0	36	1038	1515	1369	15	0
1973	131	218	125	4	2	52	538	910	612	21	10

¹ Numbers of grilse and total fish (i.e., grilse plus large salmon) captured in fence trap. Data from Table 1 in Jessop (1986).

² Numbers of salmon by sea-age category in representative aged sample of fish collected in fence trap. Numbers of virgin 1SW salmon are from Table 3 in Jessop (1986) while numbers of virgin 2SW and 3SW salmon in aged samples were provided by B. M. Jessop (Department of Fisheries and Oceans, Halifax, Nova Scotia, pers. comm.).

³ Number of previous spawners.

⁴ Estimated numbers of grilse and total fish in the river return. Data from Table 6 in Jessop (1986).

⁵ Total river returns of untagged virgin salmon categorized by sea age. Estimates were based on representation in aged sample and numbers of grilse and older salmon (i.e., total) returning to the river, e.g., number of 1SW = col. 10 = [col. 4/(col. 4 + col. 5 + col. 6 + col. 7)] X (col. 3) X (col. 8/col. 2).

Table 12. Location, method and sea age of tag recaptures from 30542 wild smolts of Big Salmon River, 1967 to 1971.

Recapture		Sea age at first recapture			
Location	Method	0SW	1SW	2SW ²	3SW ²
river	trap ¹	-	71	6	7
	recr.	1	16	16	2
	other	1	0	0	0
	total	2	87	22	9
sea-N.S.	comm.	11	2	1	0
-N.B.	comm.	24	2	4	0
-NFLD	comm.	0	0	1	0
-UNK	comm.	0	1	1	0
	total	35	5	7	0
river plus sea		37	92	29	9

¹ Trap counts incomplete as indicated by small size of some 2SW salmon recaptured in trap and fisheries, and high recreational catch efficiency of tagged salmon returning to river in 1969 (i.e., 19 of 25 recaptures in river were in recreational fishery).

² Recaptures designated virgin 2SW and 3SW salmon believed to include some previous spawners.

Table 13. Survival and natural mortality rates for untagged smolts of Big Salmon River, 1966 to 1971. Estimates of survival include salmon catches by the sea fisheries and returns to the river, whereas rates of natural mortality represent loss between the smolt stage and sea age of 12 months.

Smolt year	Smolt number ¹	Returns to river ²			% Survival ³	% Natural mortality ⁴
		1SW	2SW	3SW		
1966	18370	940	152	0	7.7	91.9
1967	(7250) ⁵	(1228) ⁵	(118) ⁵	(0) ⁵	(23.8) ⁵	(75.2) ⁵
1968	15921	108	20	0	1.0	98.9
1969	9638	731	5	0	9.7	90.1
1970	19766	563	15	10 ⁶	3.8	96.1
1971	18384	1312	20	3 ⁶	9.2	90.5
Com- bined	82079 ⁷ (89329) ⁷	3654 ⁷ (4882) ⁷	212 ⁷ (330) ⁷	13 ⁷ (13) ⁷	6.0 ⁷ (7.5) ⁷	93.7 ⁷ (92.2) ⁷

¹ Number of untagged smolts (Jessop 1975).

² From Table 11 except that returns have been reduced by numbers of salmon originating from tagged smolts of hatchery and wild origin.

³ % survival includes both total returns to river and catches of 1SW and MSW salmon in sea fisheries which were estimated from tag recaptures; 5% of the recaptures as 1SW salmon were recovered in the sea fisheries and 18% of the recaptures as MSW salmon.

⁴ % loss to natural mortality was determined by back-calculating to sea age of 12 months estimates of mortalities caused by sea fisheries and returns to the river, assuming a mean monthly natural mortality rate of 0.01 (Doubleday et al. 1979). Mean dates assumed in adjustments for natural mortality, as indicated by tag recaptures, were June 1 for entry of smolts to sea (Jessop 1975), September 1 for returns of all sea ages to river (Jessop 1986), and September 1 and July 15 for catches of 1SW and MSW salmon, respectively in sea fisheries.

⁵ Irregularity suspected in data series pertaining to 1967 smolt class; estimates of survival and natural mortality assumed to be either biased or anomalies to rates which typify this population. See text for explanation.

⁶ Based on mean proportion of 3SW salmon among returns from previous five smolt classes.

⁷ Data for 1967 smolt class included.

Table 14. Distributions of recaptures and catches from tagged and untagged smolts of Sand Hill River, 1969 to 1971. Tag recapture information are from Pratt et al. (1974) and T. R. Porter (Department of Fisheries and Oceans, St. John's, Newfoundland, pers. comm.).

Smolt year	Sea age (months)	Location ¹	Number of salmon	
			Tagged ²	Untagged ³
1969	12.5	Canada	15	1900
	13	river	32	3528
	14	Greenland	4	523
	24	Canada	35	4574 ⁴
	24	river	4	235 ⁴
	26	Greenland	1	131 ⁴
	36	river	0	1 ⁴
Total			10952	
1970	12.5	Canada	35	2051
	13	river	74	3413
	14	Greenland	47	2754
	24	Canada	48	2813 ⁴
	24	river	2	149 ⁴
	26	Greenland	1	59
	36	Canada	1	59 ⁴
	36	river	0	1 ⁴
Total			11358	
1971	12.5	Canada	16	1995
	13	river	16	1862
	14	Greenland	7	873
	24	Canada	30	3740 ⁴
	24	river	7	430 ⁴
	36	Canada	1	125 ⁴
	36	river	0	2 ⁴
Total			9027	

¹ Designates location of capture as: river - counting fence on home river; Canada - coastal net fisheries in Canada; Greenland - drift net fishery at Greenland.

² Tagged salmon returning to river or reported to have been recovered in fisheries.

³ Counts of untagged salmon returning to river and estimates of untagged salmon recaptured in fisheries. Estimates of salmon caught in fisheries were derived assuming a tag reporting rate of 0.8 and the untagged to tagged salmon ratio in the river for returns from the corresponding smolt class.

⁴ Estimated from large salmon count and an assumed age distribution of a pooled sample of 640 large salmon from several years captured in fence trap (Pratt et al. 1974). Within sample representation was 89.5% 2SW salmon, 0.5% 3SW salmon and 10.0% previous spawners.

Table 15. Survival and natural mortality rates for untagged smolts of Sand Hill River, 1969 to 1971. Estimates of survival include salmon catches by sea fisheries and returns to river, whereas rates of natural mortality represent loss between the smolt stage and sea age of 12 months.

Smolt year	Smolt number ¹	Survival		% Natural mortality ⁴
		Number ²	% ³	
1969	47859	10952	22.9	74.0
1970	42480	11358	26.7	69.9
1971	44680	9027	20.2	76.6
Combined	135019	31337	23.2	73.6

¹ Number of untagged smolts (Pratt et al. 1974).

² From table 14.

³ Number of untagged 1SW and MSW salmon caught in fisheries and returning to river expressed as a percentage of untagged smolts.

⁴ % natural mortality to sea age of 12 months determined by assuming a non-catch fishing mortality rate of 0.1 (Anon. 1981, 1986a) and a monthly mean natural mortality rate of 0.01 (Doubleday et al. 1979).

Table 16. Returns of maturing salmon by sex and sea age to Big Salmon River, 1968 to 1972. Numbers of 1SW virgin salmon were estimated by method described in table 11. The remaining salmon in total returns to the river (i.e., the MSW salmon and previous spawners) were partitioned into different sea-age classes according to age distribution of sample taken at counting fence and for which length measurements were recorded (see appendix A in Jessop 1986). Numbers in parentheses represent aged sample.

Sex	Sea age ¹	Year of return					Total
		1968	1969	1970	1971	1972	
male	1.0	451 (163)	56 ² (9)	298 (107)	194 (79)	395 (143)	1394
	2.0	15 (15)	13 (3)	2 (1)	2 (1)	0 (0)	32
	3.0	6 (2)	0 (0)	0 (0)	0 (0)	0 (0)	6
	Subtotal	472	69	300	196	395	1437
	2.1	214 (75)	304 (70)	42 (19)	19 (10)	34 (13)	613
	3.2	26 (75)	9 (2)	9 (4)	0 (0)	0 (0)	44
	3.1,2	54 (19)	56 (13)	83 (38)	7 (4)	0 (0)	200
	4.2,3	3 (1)	4 (1)	0 (0)	0 (0)	0 (0)	7
	4.1,2,3	0 (0)	9 (2)	4 (2)	17 (9)	3 (1)	33
	Subtotal	297	382	138	43	37	897
Total		769	451	438	239	432	2329

female	1.0	820 (296)	56 ² (4)	437 (157)	376 (153)	974 (352)	2663

2.0	140 (48)	132 (31)	19 (8)	3 (2)	15 (3)	309
3.0	23 (8)	0 (0)	0 (0)	0 (0)	0 (0)	23
Subtotal	983	188	456	379	989	2995
2.1	550 (193)	622 (143)	46 (21)	50 (24)	57 (21)	1325
3.2	99 (35)	52 (12)	85 (39)	4 (2)	3 (1)	243
3.1,2	191 (67)	200 (46)	416 (190)	30 ³ (27)	13 (5)	850
4.2,3	0 (0)	52 (12)	15 (7)	4 (2)	0 (0)	71
4.1,2,3	77 (27)	43 (10)	116 (53)	138 (67)	21 (8)	395
5.2,3,4	0 (0)	0 (0)	7 (3)	0 (0)	0 (0)	7
5.1,2,3, 4	34 (12)	13 (3)	22 (10)	26 (13)	0 (0)	95
6.1,2,3, 4,5	0 (0)	9 (2)	2 (1)	2 (1)	0 (0)	13
7.1,2,3, 4,5,6	0 (0)	0 (0)	2 (1)	0 (0)	0 (0)	2
Subtotal	951	991	711	254	94	3001
Total	1934	1179	1167	633	1083	5996

Male and female	Grand total	2703	1630	1605	872	1515	8325
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¹ Sea age designations by number of years since smolt stage (i.e., 1 to 7) and according to spawning history, e.g., a 4.1,2,3 salmon entered the sea 4 years prior and has spawned previously after 1, 2 and 3 years since smolt stage.

² Total returns of 1SW salmon were partitioned into male and female categories assuming a 50:50 sex ratio because sample was small (13 fish) and sex ratio of aged sample deviated from that of 1SW salmon returns in other years.

³ Reduced to 30 salmon because original estimate of 50 salmon seemed biased when compared with estimate of returns of the same fish in previous years. The 20 salmon removed from this age category were partitioned among the large salmon according to aged sample.

Table 17. Mortality between spawning and subsequent return to Big Salmon River. Estimates based on data presented in Table 16 and assuming all successive spawning occurred in consecutive years.

Successive return years (Yr _i , Yr _{i+1})	Total return ₁ yr _i	Sport catch yr _i	Spawning escapement yr _i	Total return ₁ yr _{i+1}	% Mort- ality ²
1968,69	2703	291	2412	1373	43.1
1969,70	1630	529	1101	849	22.9
1970,71	1605	491	1114	297	73.3
1971,72	872	266	606	131	78.4
Combined	6810	1577	5233	2650	49.4

¹ Returns of all sea ages (Table 16).

² % mortality = $[1 - (\text{total return in yr}_{i+1} / \text{spawning escapement in yr}_i)] \times 100$.

Table 18. Mortality between spawning and subsequent return to Big Salmon River according to sex and number of spawnings. Estimates of spawning escapements are for 1968 to 1972.

Sex	Successive spawning times ¹	Total return ² yr _i	Sport catch ³ yr _i	Spawning escapement ⁴ yr _i	Total return ² yr _{i+1}	% Mortality ⁵
male	1 and 2	1037	253	784	417	46.8
	2 and 3	623	146	477	150	68.6
	3 and 4	207	46	161	33	79.5
	4 and 5	30	7	23	0	100.0
female	1 and 2	2006	473	1533	919	40.1
	2 and 3	1508	337	1171	730	37.7
	3 and 4	908	213	695	329	52.7
	4 and 5	381	79	301	61	79.7
	5 and 6	95	18	77	13	83.1
	6 and 7	13	3	10	2	80.0
	7 and 8	2	0	2	0	100.0
males and females	1 and 2	3043	726	2317	1336	42.3
	2 and 3	2131	483	1648	880	46.6
	3 and 4	1115	259	856	362	57.7
	4 and 5	411	86	325	61	81.2
	5 and 6	95	18	77	13	83.1
	6 and 7	13	3	10	2	80.0
	7 and 8	2	0	2	0	100.0

¹ Spawned in yr_i and yr_{i+1}.

² Total returns by sex and sea age (Table 16).

³ Sport catches of grilse and large salmon were partitioned into age classes using distribution of aged sample collected at counting fence and an adjustment to correct for different proportions of grilse in total return to river and harvested in sport fishery. Numbers of virgin 1SW salmon taken in sport fishery = (total river return of virgin 1SW salmon/total river return of grilse) X sport catch of grilse. Number of salmon from an older age class in sport catch = [number from older age class in aged sample/(total number in aged sample - number of 1SW salmon in sample)] X (total sport catch - 1SW salmon in sport catch).

⁴ Spawning escapement in yr_i = total return in yr_i - sport catch in yr_i.

⁵ % mortality = [1 - (total return in yr_{i+1}/spawning escapement in yr_i)] X 100.

Table 19. Estimates of grilse (<63 cm) and large salmon (>63 cm) returning to the LaHave River from wild smolts produced above Morgan Falls, New Germany.

Size class	Year of return	Tag recaptures			Returns		
		Morgan Falls	Sport fishery	Exploit'n rate ¹	Morgan Falls ²	Sport fishery ³	River ⁴
1	2	3	4	5	6	7	8
grilse	1978	26	2	.071	275	21	296
	1979	77	21	.214	856	233	1089
	1980	44	12	.214	1637	466	2083
	1981	185	78	.297	1866	787	2653
	1982	75	16	.176	799	170	969
	1983	-	-	(---) ⁵	1129	43 ⁶	1172
	1984	-	-	(.249) ⁷	2043	678	2721
	1985	24	14	.368	1343	783	2126
large salmon	1978	43	8	.157	67	12	79
	1979	3	2	(.214) ⁸	67	18	85
	1980	72	17	.191	288	68	356
	1981	32	13	.289	366	149	515
	1982	29	10	.256	256	88	344
	1983	21	3	.125	213	30	243
	1984	-	-	(.100) ⁹	384	43	427
	1985	-	-	(.037) ¹⁰	638	25	663

¹ Exploitation rate = col. 4 / (col. 3 + col. 4).

² Counts of grilse and large salmon through fishway at Morgan Falls (Cutting and Jefferson 1986).

³ Sport fishery catch = [col. 6 / (1 - col. 5)] - col. 6.

⁴ Total returns to river = col. 6 + col. 7.

⁵ Not possible to determine from tag recaptures in other years or from rate for large salmon because low summer flows contributed to abnormally low grilse catch for river.

⁶ Contribution made to 1983 sport catch by grilse from wild smolts of upper LaHave River was determined by multiplying total angling catch of grilse in 1983 for river (i.e., 130) by mean proportionate contribution (i.e., 0.33) made by upper river population to total catches in previous four years (i.e., 1979 to 1982). Sport catches are from O'Neil and Swetnam (1984) and Swetnam and O'Neil (1984).

⁷ Mean exploitation rate for 1SW salmon returning 1978 to 1985.

- ⁸ Because of few tag recaptures as large salmon, exploitation rate assumed equal to rate for grilse in same year.
- ⁹ Represents kill rate by sport fishery for large salmon returning to river. Rate equals mean exploitation rate for large salmon returning from 1978 to 1983, reduced by proportion of catch in 1984 that survived release. Forty-two percent of 298 large salmon caught in 1984 were released (O'Neil et al. 1985), and 10% of released fish were assumed to have died (Cutting and Jefferson 1986).
- ¹⁰ Represents kill rate of large salmon determined as 10% of exploitation rate derived for grilse in same year. Regulations prohibited retention of large salmon.

Table 20. Sample aging data for wild salmon passed through counting trap at Morgan Falls, LaHave River. Data represent age distributions within size classes for grilse (<63cm) and large salmon (>63cm) (J. D. Cameron, Department of Fisheries and Oceans, Halifax, Nova Scotia, pers. comm.).

Year	Grilse			Large salmon			
	Total	1SW	Cons.PS ¹	Total	2SW	Cons.PS ¹	Alt.PS ²
1978	28	28	0	17	10	0	7
1979	82	82	0	22	16	1(1) ³	5(1) ³
1980	140	139	1	92	80	2(1) ³	10(2) ³
1981	281	270	11	96	80	3	13
1982	45	42	3	58	31	2(1) ³	25
1983	192	190	2	133	81	5(1) ³	47(1) ³
1984	248	228	20	67	40	8(2) ³	19(9) ³
1985	213	206	7(1) ³	389	323	9(1) ³	57(1) ³

¹ Previous spawners that spawned in the previous year, i.e., consecutive-year spawners.

² Previous spawners that last spawned two years previous, i.e., alternate-year spawners.

³ Number in parentheses represents previous spawners that had spawned twice.

Table 21. Mortality between spawning and subsequent return to river for wild salmon of upper LaHave River.

Year of spawning Yr_1	Spawning escapement Yr_1	Cons. spawner ² returns Yr_{i+1}		Alt. spawner ² returns Yr_{i+2}		% Mort- ⁵ ality
		Number	% return ³	Number	% return ⁴	
1978	342	4	1.2	39	11.4	87.4
1979	923	23	2.5	70	7.6	89.9
1980	1925	120	6.2	148	7.7	86.1
1981	2232	77	3.4	86	3.9	92.7
1982	1055	21	2.0	121	11.5	86.5
1983	1342	270	20.1	97	7.2	72.7
Combined	7819	515	6.6	561	7.2	86.2

¹ Grilse and large salmon counted at Morgan Falls in Yr_i (see Table 19).

² Consecutive-year (Cons.) or alternate-year (Alt.) spawners present in angling catches and spawning escapements. Estimates derived using aging data (Table 20) to partition total returns to river (Table 19).

³ % return = (number of returns in Yr_{i+1} /spawning escapement in Yr_i) X 100.

⁴ % return = (number of returns in Yr_{i+2} /spawning escapement in Yr_i) X 100.

⁵ % mortality = $[1 - (\text{number of cons. spawner returns in } Yr_{i+1} + \text{number of alt. spawner returns in } Yr_{i+2}) / \text{spawning escapement in } Yr_i] \times 100$.

Table 22. Five years of Miramichi River smolt tagging and recapture data with tagging dates and minimum water temperatures ($^{\circ}\text{C}$).

Smolt year	Number tagged	Number recaptured	Tagging date		Minimum temperature
			Calendar	Julian	
1969	211	7	May 26	146	8.3
	338	5	May 27	147	11.1
	299	7	May 28	148	10.6
	201	8	May 29	149	11.1
	274	8	May 30	150	9.2
	900	41	Jun 2	153	10.8
	897	37	Jun 3	154	12.2
	900	18	Jun 4	155	13.3
	1000	16	Jun 5	156	12.8
	600	18	Jun 6	157	14.4
	900	13	Jun 9	160	14.4
	700	14	Jun 10	161	15.6
	600	5	Jun 11	162	16.1
	400	3	Jun 12	163	16.1
1970	137	2	May 23	143	8.9
	346	5	May 25	145	11.1
	617	8	May 26	146	10.6
	300	2	May 27	147	10.0
	571	13	May 29	149	8.9
	600	16	May 30	150	10.0
	565	20	Jun 2	153	12.2
	533	10	Jun 3	154	12.8
	367	4	Jun 4	155	12.8
	160	5	Jun 5	156	14.4
	671	18	Jun 6	157	12.2
	485	4	Jun 7	158	15.0
	224	2	Jun 9	160	13.3
	169	4	Jun 10	161	14.2
	352	5	Jun 15	166	15.0
	367	4	Jun 16	169	16.1
1974	229	13	Jun 6	157	11.7
	127	8	Jun 7	158	11.7
	515	24	Jun 10	161	12.2
	528	18	Jun 11	162	15.0
	167	6	Jun 12	163	13.3
	415	11	Jun 13	164	12.8
	319	10	Jun 14	165	13.9
	155	3	Jun 16	167	16.1
	709	9	Jun 17	168	16.7
	143	0	Jun 18	169	16.1

	120	0	Jun 24	175	17.8
1975	387	10	May 26	146	7.2
	220	5	May 27	147	10.0
	264	3	May 29	149	8.9
	142	0	May 30	150	10.0
	496	10	Jun 2	153	12.2
	397	4	Jun 3	154	12.2
	347	5	Jun 4	155	14.4
	589	6	Jun 5	156	12.2
	269	2	Jun 6	157	12.2
	100	1	Jun 12	163	8.9
	200	2	Jun 13	164	13.3
	200	0	Jun 20	171	15.6
	100	1	Jun 21	172	16.7
1976	118	0	May 24	145	6.7
	185	1	May 25	146	6.7
	194	1	May 28	149	8.9
	358	3	May 30	151	11.7
	404	4	May 31	152	14.4
	418	7	Jun 2	154	11.1
	242	3	Jun 3	155	14.4
	266	6	Jun 4	156	14.4
	251	6	Jun 7	159	14.4
	689	16	Jun 8	160	14.4
	552	9	Jun 9	161	12.2
	133	0	Jun 10	162	15.6
	323	3	Jun 13	165	16.7

Table 23. Results of weighted regression analyses of tag recapture rate for wild smolts on tagging date and minimum estuarial temperature, Miramichi River.

Independent variable	Smolt year	Regression type	Degrees of freedom ¹	F-value	Prob.
tagging date	1969	parabolic	2,11	6.70	0.012
	1970	parabolic	2,13	2.91	0.089
	1974	linear	1, 9	52.47	<0.001
	1975	linear	1,11	7.34	0.021
	1976	parabolic	2,10	9.05	0.006
minimum temperature	1969	linear	1,12	7.41	0.018
	1970	-	-	-	>0.100
	1974	linear	1, 9	21.75	0.003
	1975	linear	1,11	4.06	0.070
	1976	-	-	-	>0.100

¹Degrees of freedom in residual mean square.

Table 24. Tagging and recapture data with release dates for thirteen groups of hatchery smolts released into LaHave River, 1978 to 1981.

Smolt year	Number released	Number recaptured	Release date	
			Calendar	Julian
1978	3894	61	Apr 23	113
	2414	31	Apr 24	114
	4890	73	Apr 27	117
	3928	84	May 14	134
	2399	41	May 14	134
1979	1996	50	May 2	122
	1999	43	May 2	122
1980	1998	43	Apr 28	119
	1998	30	May 12	133
	1987	30	May 26	147
1981	2993	79	May 12	132
	2981	38	Jun 3	154
	1991	17	Jun 4	155

Table 25. Nominal catches and anomalies to base-year catches for small and large salmon harvested in 1978 and 1979, respectively. Base-year catches are the means of catches in the two years both preceding and following 1978 or 1979. Recreational and commercial catches are partitioned under 33 geographical areas. Each catch anomaly is expressed as a percent of the mean of catches for the base-years. Catches exceeding 90% confidence intervals of catches for the base-years plus 1978 or 1979 are marked with an asterisk (*).

Geograph- ical area	Catch/ anomaly	Small salmon in 1978		Large salmon in 1979	
		Recr.	Comm.	Recr.	Comm.

USA					
Maine					
Narraguagus R. ¹					
	catch			20*	
	anomaly			-69	
Canada					
New Brunswick ²					
Lower Fundy					
	catch	424*		525 ₉	
	anomaly	-80		-72 ₉	
Upper Fundy					
	catch	419			
	anomaly	-27			
Nova Scotia ²					
Upper Fundy					
	catch	1612			
	anomaly	+85			
Lower Fundy					
	catch			9	
	anomaly			-65	
Southwest					
Shore					
	catch	338*		275*	1057*
	anomaly	-84		-57	-60
Eastern					
Shore					
	catch	300*		202*	432*
	anomaly	-84		-39	-66
Cape Breton					
East					
	catch	169		200*	864*
	anomaly	-56		-47	-76
Gulf					
	catch	30 ₇		159*	1501*
	anomaly	-66 ₇		-56	-70
New Brunswick ²					
Miramichi					
	catch	5364		2441 ₉	
	anomaly	-44		-70 ₉	

Restigouche	catch	1467*		1037*	
	anomaly	-45		-77 ⁹	
Quebec ³					
Gaspe	catch	996*		929*	
	anomaly	-51		-78	
Anticosti	catch	76*		136*	
	anomaly	-78		-87	
Upper North Shore	catch	1095		907*	3194*
	anomaly	-3		-54	-62
Lower North Shore	catch	793		650	4499
	anomaly	0		-18	-39
Newfoundland ⁴					
Area N	catch	1350*	1268*		477*
	anomaly	-47	-77		-56
Area M	catch	1800*	6046		926*
	anomaly	-43	-29		-41
Area L	catch	2962 ⁸	2735 ⁸		476 ⁸
	anomaly	-17 ⁸	-51 ⁸		-59 ⁸
Area K	catch	2327 ⁸	7401 ⁸	84*	1462 ⁸
	anomaly	-31 ⁸	-33 ⁸	-86 ⁸	-42 ⁸
Area J ₂	catch	505 ⁸	1055 ⁸		12077* ⁸
	anomaly	-65 ⁸	-78 ⁸		-29 ⁸
Area J ₁	catch	2420 ⁸	1297 ⁸		6250* ⁸
	anomaly	+13 ⁸	-86 ⁸		+75 ⁸
Area I	catch	1437	4210		1029*
	anomaly	+3	-27		-49
Area H	catch	1595*	7416		3106
	anomaly	+52	-34		-25
Area G	catch	1303	3702		1239
	anomaly	-23	-35		+88
Area F	catch	44*	1487*		1881*
	anomaly	-54	-80		-81
Area E	catch	99	4771		1418*
	anomaly	+18	-40		-87

Area D	catch	296	10193		1757*
	anomaly	-2	-18		-82
Area C	catch	2858	11578		3849*
	anomaly	+8	-3		-73
Area B	catch	8774	17821		7403*
	anomaly	+8	-56		-65
Area A	catch	849*	25731*		15708*
	anomaly	-49	-69		-55
Labrador⁴					
Southern	catch	1816*	19126*	286	35794*
	anomaly	-53	-69	-45	-59
Northern	catch	875	14530	323	16444*
	anomaly	+23	+11	-7	-30
Quebec³					
Ungava ⁵	catch	231		962	
	anomaly	+16		-14	

Total-Upper ⁶ Fundy	catch	42593 ¹⁰	140367 ¹⁰	9145 ¹⁰	122843 ¹⁰
	anomaly	-29	-54	-66	-54

¹Based on reported catches of 2SW wild salmon caught in sport fishery on Narraguagus River (Anon. 1986a).

²Commercial catches for New Brunswick and Nova Scotia are from Dunfield (1977), Mitham and Bernard (1977, 1978), Smith and Bernard (1979), Swetnam and Bernard (1980, 1981) and Cutting (1984). Recreational catches are from O'Neil and Swetnam (1984) and Swetnam and O'Neil (1984).

³Catch statistics for Quebec fisheries were provided by Y. Côté, (Ministère du Loisir, de la Chasse et de la Pêche, Gouvernement du Québec, Saint-Cyrille, Québec, pers. comm.). Comparisons of large salmon catches in sport fishery limited to salmon ≥ 2.2 and < 5.4 kg.

⁴Catch statistics for Newfoundland and Labrador are mainly from O'Connell et al. (1985). Data for Statistical Areas J₂, K to N and Section 50 in Labrador were provided by T. R. Porter (pers. comm.).

⁵Includes only catches for George and Baleine rivers.

⁶Excludes catches of upper Bay of Fundy rivers because salmon of these rivers do not migrate to northwest Atlantic (see

section 2.0).

⁷ Comparison against base-years 1976 and 1977 only, because catches in 1979 and 1980 were influenced by hatchery plantings.

⁸ Catches in 1976 or 1977, or in both, excluded because season regulations pertaining to both commercial and recreational fisheries were different.

⁹ Catch in 1981 excluded because licensed commercial salmon season re-opened.

¹⁰ Catch not compared with 90% confidence limits for catch series.

Table 26. Recreational catches of grilse and surrogates of mean flows during main fishing periods for Big Salmon and Stewiacke rivers, and mean SST in Bay of Fundy during June-July of post-smolt year (SST).

Yr ₁	Big Salmon		Stewiacke		SST ⁵ Yr ₁₋₁
	Catch ₁ Yr ₁	Flow ₂ Yr ₁	Catch ₃ Yr ₁	Flow ₄ Yr ₁	
1970	358 (215) ⁶	3.46	355	13.09	11.02
1971	312 (175) ⁶	2.21	337	9.80	11.73
1972	266 (162) ⁶	2.91	343	8.13	11.97
1973	442 (370) ⁷	5.33	520	2.62	11.11
1974	301 (317) ⁸	2.30	1087 ⁹	10.31	10.73
1975	177	1.30	442 ⁹	5.49 (5.62) ¹²	11.07
1976	636	4.62	940 ⁹	12.40 (20.20) ¹²	10.62
1977	188	3.33	104 ⁹	24.18 (24.97) ¹²	12.87
1978	274	0.63	545 ⁹	1.09 (6.84) ¹²	11.21
1979	907	6.32	681 ⁹	13.31	11.12
1980	4	1.83	41 ⁹	6.76 (9.54) ¹²	11.77
1981	603	2.23	531	8.89	10.42
1982	416	3.61	307	3.33	11.22
1983	304	1.54	1033	6.82	10.82
1984	300	2.93	224 (329) ¹⁰	3.84	11.51
1985	191	1.02	564 (829) ^{10,11}	4.67 (5.66) ¹³	11.42

¹ Catch from June through September.

² Mean flow ($m^3 \cdot sec^{-1}$) from July 1 to September 30 for Point Wolfe River at Fundy National Park, gauging station 01BV006 of Inland Waters Directorate, Environment Canada (Anon. 1985d, 1986c).

³ Catch for entire season.

⁴ Mean flow ($m^3 \cdot sec^{-1}$) from September 1 to October 15, unless stated otherwise, for Musquodoboit River at Crawford Falls, gauging station 01E001 of Inland Waters Directorate, Environment Canada (Anon. 1985d, 1986c).

⁵ Mean June-July SST ($^{\circ}C$) based on twice daily readings taken at the Biological Station, Department of Fisheries and Oceans, St. Andrews, New Brunswick.

⁶ Catch adjusted for differential return due to tagging, trapping and counting smolts. Original catch, in parentheses, was first reduced by the number of tagged 1SW salmon originating from tagged smolts of either wild or hatchery origin. Numbers of tagged salmon were adjusted for a tag loss of 25% (Isaksson and Bergman 1978). Catch of untagged fish was adjusted upwards by

the proportion of the wild smolt run that was tagged in the previous year (percentage of run tagged ranged from 28 to 33%) and a handicap ratio of 1.2 to compensate for differential mortality due to trapping and counting smolts (see section 3.3.1.1 for explanation).

- ⁷Original catch in parentheses adjusted similarly to catches in previous years except that handicap ratio of 1.1 was used because smolts were counted only during part of run.
- ⁸Original catch in parentheses reduced by number of 1SW salmon from tagged hatchery smolts released into river in 1973.
- ⁹Season extended to October 31.
- ¹⁰Catch estimate determined from license stub-return system, in parentheses, was reduced by 32% to adjust for difference in estimates reported by field officers and determined from stub-return system. Adjustment based on comparisons of paired estimates of total catches determined independently by creel census and from license stub-returns for the Stewiacke River in 1983 and 1984 (S. F. O'Neil, Department of Fisheries and Oceans, Halifax, Nova Scotia, pers. comm.).
- ¹¹Season extended to October 29.
- ¹²Mean flow from September 1 to October 31.
- ¹³Mean flow from September 1 to October 29.

Table 27. Counts of smolts and resultant returns of 1SW salmon to Western Arm Brook and numbers of 1SW salmon harvested in Area N commercial fishery from smolt classes 1971 to 1983. Data are from Chadwick (1987).

Yr _i	Smolts in Yr _i	1SW salmon in Yr _{i+1}	
		River returns	Area N Commercial
1971	5734	415	2062
1972	11906	827	8428
1973	8484	526	2738
1974	12055	640	3667
1975	9733	552	4258
1976	6359	376	3922
1977	9640	317	1268
1978	13071	1576	6814
1979	9400	470	6919
1980	15675	471	7370
1981	13981	467	10799
1982	12477	1146	2432
1983	10552	238	2766

Table 28. Comparisons of sea growth for hatchery and wild smolts emigrating from LaHave River in 1977, 1978 and 1980. Bars over paired means indicate difference determined by analysis of factor effects and the Bonferonni method of multiple comparisons (Neter et al. 1985). Significance of difference for pair-wise comparisons was based on 95% confidence intervals. Broken bars represent difference within hatchery or wild components, whereas solid bars indicate difference within the combined responses for both population components.

Measurement		Mean/ SD ¹	Fork length measurements (cm)					
			Hatchery			Wild		
Type	Period		1977	1978	1980	1977	1978	1980
1SW salmon length	-	Mean	53.63	52.28	53.54	52.60	52.30	54.26
		SD	2.08	2.63	2.33	2.36	1.97	2.12
length incr ² ment	annual ³	Mean	31.86	32.30	33.20	33.88	34.79	35.83
		SD	2.11	2.96	2.22	2.66	1.95	2.31
length incre- ment per circulus ⁴ spacing	annual ³	Mean	.901	.908	.923	.924	.933	.963
		SD	.051	.058	.057	.058	.067	.050
	summer- fall ⁵	Mean	.943	.978	.999	.991	1.050	1.064
		SD	.062	.072	.070	.075	.083	.067
	winter- spring ⁶	Mean	.827	.804	.817	.812	.782	.823
		SD	.054	.066	.060	.068	.080	.059

¹Standard deviation.

²1SW salmon length minus smolt length.

³From smolt to 1SW salmon return.

⁴Fork length increment divided by number of circuli for growth period.

⁵For first 16 circuli of sea growth.

⁶For final 20 circuli of sea growth.

Table 29. Comparison of summer-fall growth rate in first sea-year for 1977 smolt class with comparable rates for 1976 and 1978 to 1986 smolt classes. Growth rate is represented by the mean length increase per circulus spacing for the first 16 circuli of sea growth.

Smolt class i	Length increment (cm)		
	Mean	SD ¹	Difference ²
1976	1.045	.093	-0.054
1977	.991	.075	-
1978	1.050	.083	-0.059
1979	1.045	.081	-0.054
1980	1.064	.067	-0.073*
1981	1.091	.075	-0.100*
1982	1.111	.062	-0.120*
1983	1.081	.071	-0.090*
1984	1.108	.091	-0.117*
1985	1.072	.062	-0.081*
1986	1.113	.064	-0.122*

¹ Standard deviation.

² Difference between mean length increments for smolt classes 1977 and i, respectively.

*Asterisk indicate statistical difference as determined by analysis of factor effects and the Bonferonni method of multiple comparisons (Neter et al. 1985), and based on 95% confidence intervals.

Table 30. Numbers and potential sources of salmon tags recovered from cormorant rookeries on Tabacco and Indian islands, Nova Scotia. See figure 6 for locations of rookeries and rivers into which tagged hatchery smolts were released.

Location of rookery	Smolt releases			Number recovered
	River	Year	Number	
Tabacco Is.	Liscomb	1986	4000	9
		1985	1993	0
		1984	3990	0
		1983	6000	1
		1982	9983	0
		1981	9200	1
	St. Mary's	1986	5987	146
		1985	3998	2
Indian Is.	LaHave	1986	22000	20
		1985	7996	2
		1984	14970	9
		1983	11941	1
		1981	7965	0
		1984	1995	0
	Petite	1985	5991	1
	Medway	1984	5998	0
		1983	9935	0
		1982	4000	0
		1981	10962	0

Table 31. Recreational catches of grilse for selected rivers or areas, 1972 to 1986. Correlation coefficients (r) were determined by correlating catch with year of catch.

Catch year	Stew- 1 iacke	Big 1 Salmon	Mira- 2 michi	Gaspe 3	Quebec 4 N.Shore	Newfoundland-Labrador			
						Areas 5 A-F	Areas 6 G-J	Areas 7 K-N	Area 8 O
1972	343	266	19101	876	940	2601	7664	10818	2947
1973	520	442	13858	972	1544	3775	9566	16550	7492
1974	1087	301	18232	814	1118	2963	7945	10278	2501
1975	442	177	15598	1104	1834	3316	7370	16775	3972
1976	940	636	27182	1240	1662	3202	6845	17672	5726
1977	104	188	13590	1464	1487	6706	6955	12276	4594
1978	545	274	8265	758	2100	4055	7284	8439	2691
1979	681	907	14508	1306	2369	3840	6867	12461	4118
1980	41	4	11997	2575	2474	4987	9848	11580	3800
1981	531	603	22716	2770	5373	6651	11435	15035	5191
1982	307	416	21402	1144	2823	5595	12099	14276	4104
1983	1033 ⁸	304	8390 ¹⁰	580	978	4450	8927	10005	4372
1984	224 ⁸	300	10659 ¹⁰	875	1967	4191	12817	12520	2901
1985	564 ⁸	191 ⁹	18439	900	2020 ¹¹	5438	10091	8840	3101
1986	291 ⁸	108 ⁹	26163	1990	N/A ¹¹	5510	10317	12011	3465
1972-86									
Mean ¹²	510	341	16673	1291	2049	4485	9069	12636	4065
C.V.	62	68	36	51	54	29	22	23	33
r	-0.181	-0.153	+0.040	+0.236	+0.383	+0.609*	+0.636*	-0.307	-0.262
1977-86									
Mean ¹²	432	330	15613	1436	2399	5142	9664	11744	3834
C.V.	69	79	40	53	52	20	22	18	21
r	+0.140	-0.254	+0.045	-0.097	-0.026	-0.036	+0.667*	-0.041	-0.294

¹From Table 26 except catch in 1986 which is from O'Neil et al. (1987).

²Data from Randall and Schofield (1987).

³Data from Landry (1987).

⁴Data provided by Y. Côté (pers. comm.).

⁵Data from O'Connell et al. (1987). Catches from Area B excluded because their increase since 1972 is believed due to stock enhancement on Exploits River.

⁶Data from O'Connell et al. (1987) and Pepper and Mullin (1987).

⁷Data from Pepper and Mullin (1987).

⁸Recreational catch, from license stub-return system, was reduced by 32% to adjust for difference in estimates reported by field officers and determined from stub-return system. Adjustment factor provided by S. F. O'Neil (pers. comm.).

⁹Includes June-September catches only, as do catches reported for previous years.

¹⁰Catch estimate based on 2833 angler reports to Department of Fisheries and Oceans (i.e., 18% of licensees in 1984), obtained in response to a February survey of 50% of license holders (Newbould and O'Neil 1989).

¹¹Not available.

¹²Coefficient of variation.

*significant at $p < 0.05$.

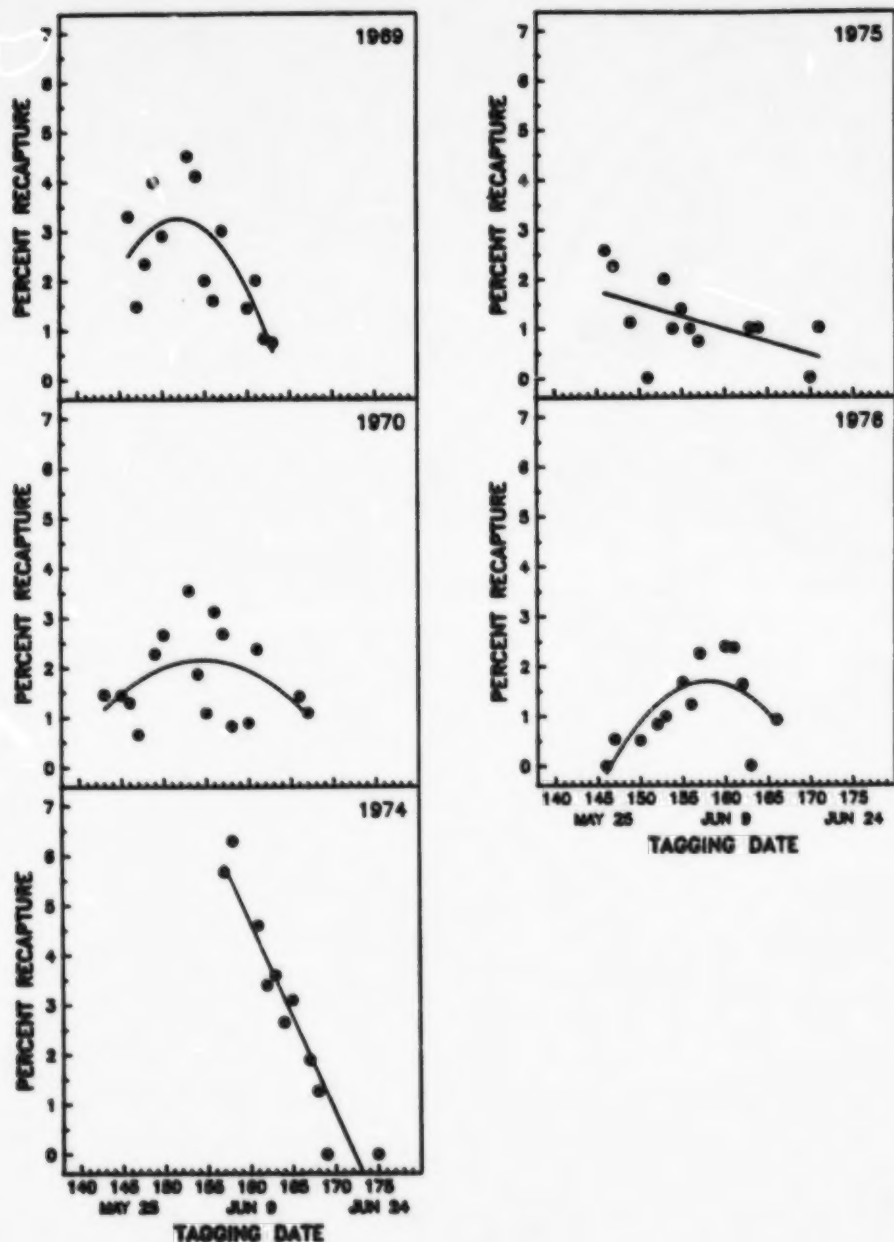


Fig. 2. Plots of percent tag recaptures for wild smolts of the Miramichi River against tagging date (i.e., time of migration). Year of smolt migration is indicated in upper corner. Tagging date is indicated by both calendar date and Julian day. Lines fitted to recapture percentages by unweighted regression.

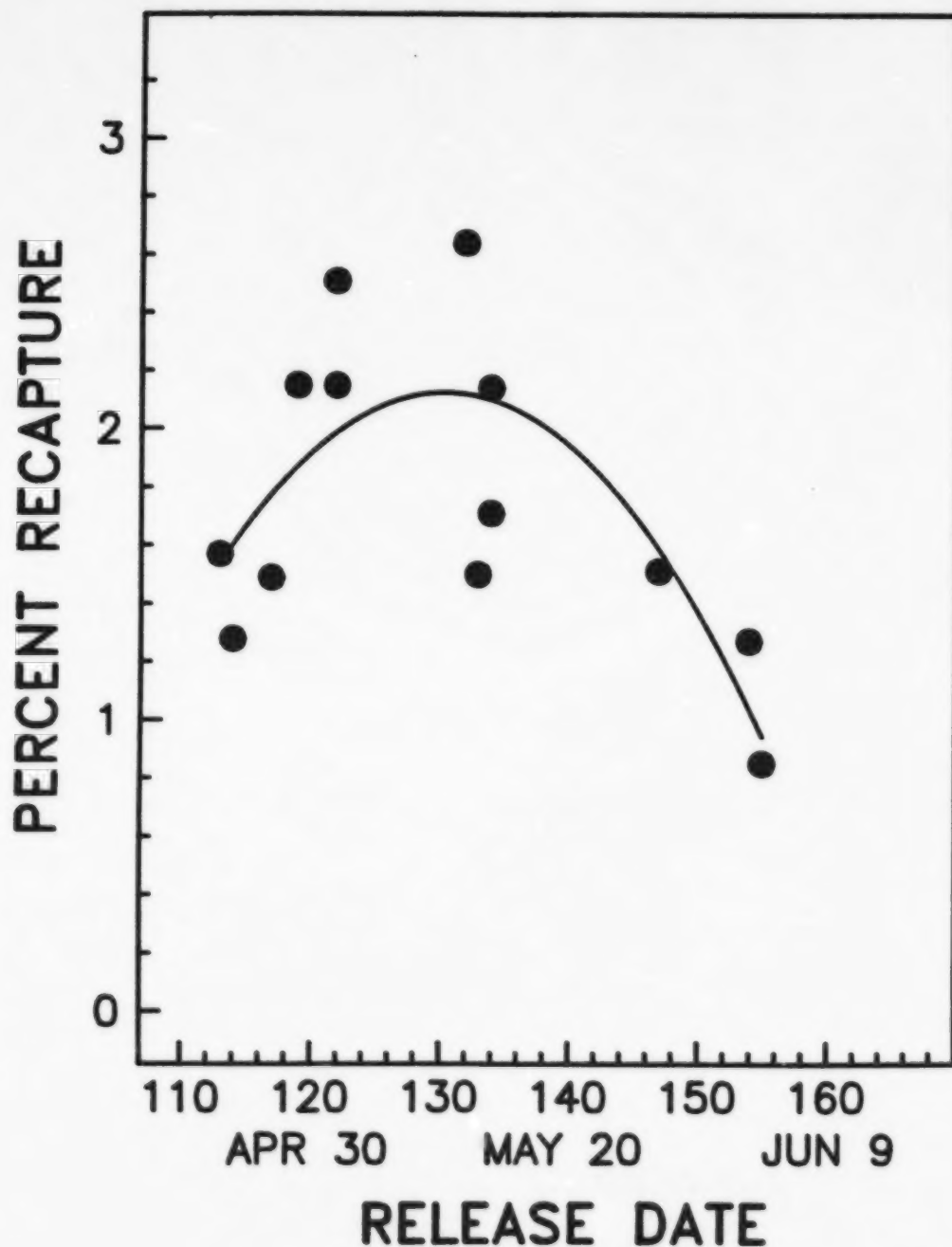


Fig. 3. Plot of percent tag recaptures for hatchery smolts against release date. All smolts released into LaHave River, 1978 to 1981. Release date is indicated by both calendar date and Julian day. Line fitted to recapture percentages by unweighted regression.

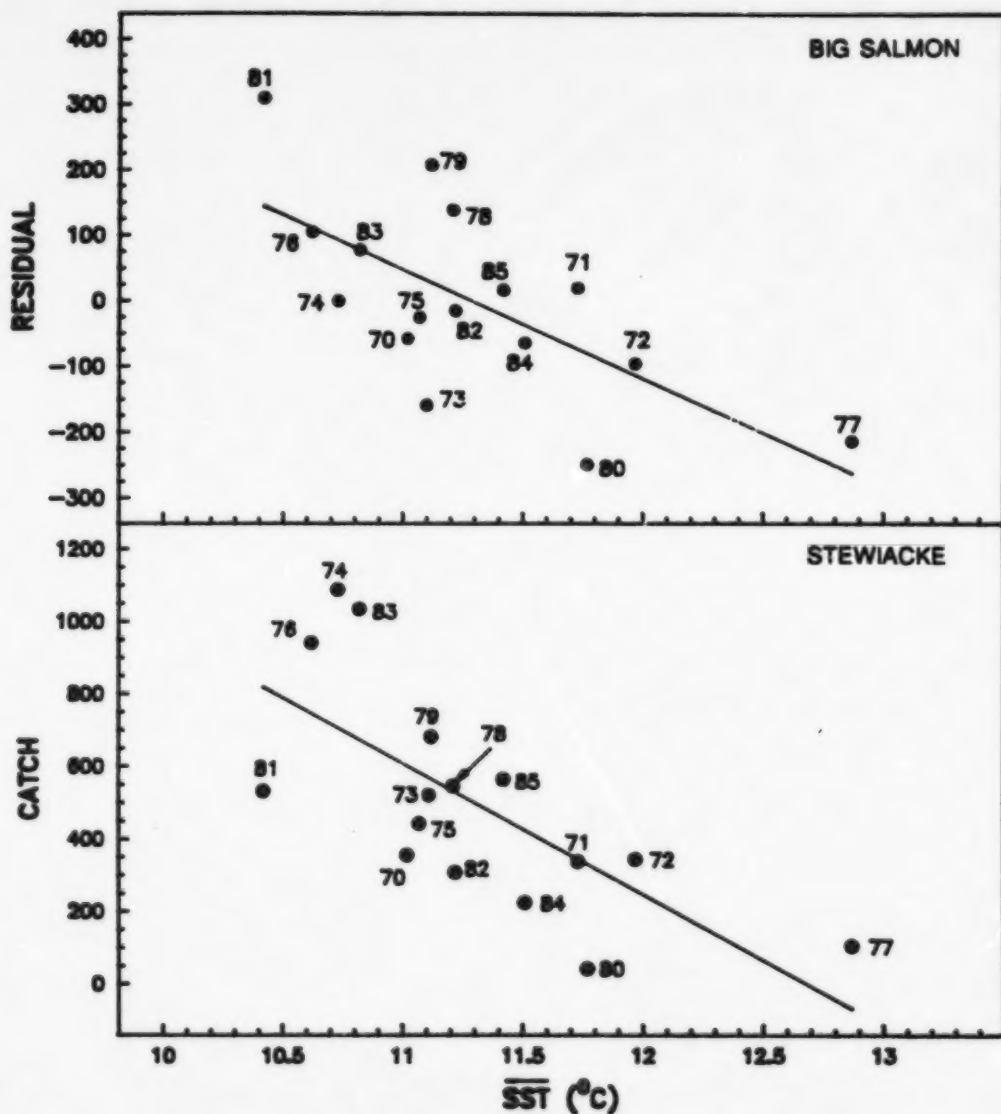


Fig. 4. Relationships between indices of LSW salmon production for populations of Big Salmon and Stewiacke rivers and mean SST in the Bay of Fundy during June-July of post-smolt year ($\overline{SST}$). Production index for Big Salmon is the residual from regression of annual recreational catch of grilse for June to September on a surrogate of mean river flow for July to September, whereas index for Stewiacke is the annual recreational catch of grilse. Catch year is identified with each point and mean sea temperatures were derived from twice daily readings at Biological Station, St. Andrews, New Brunswick.

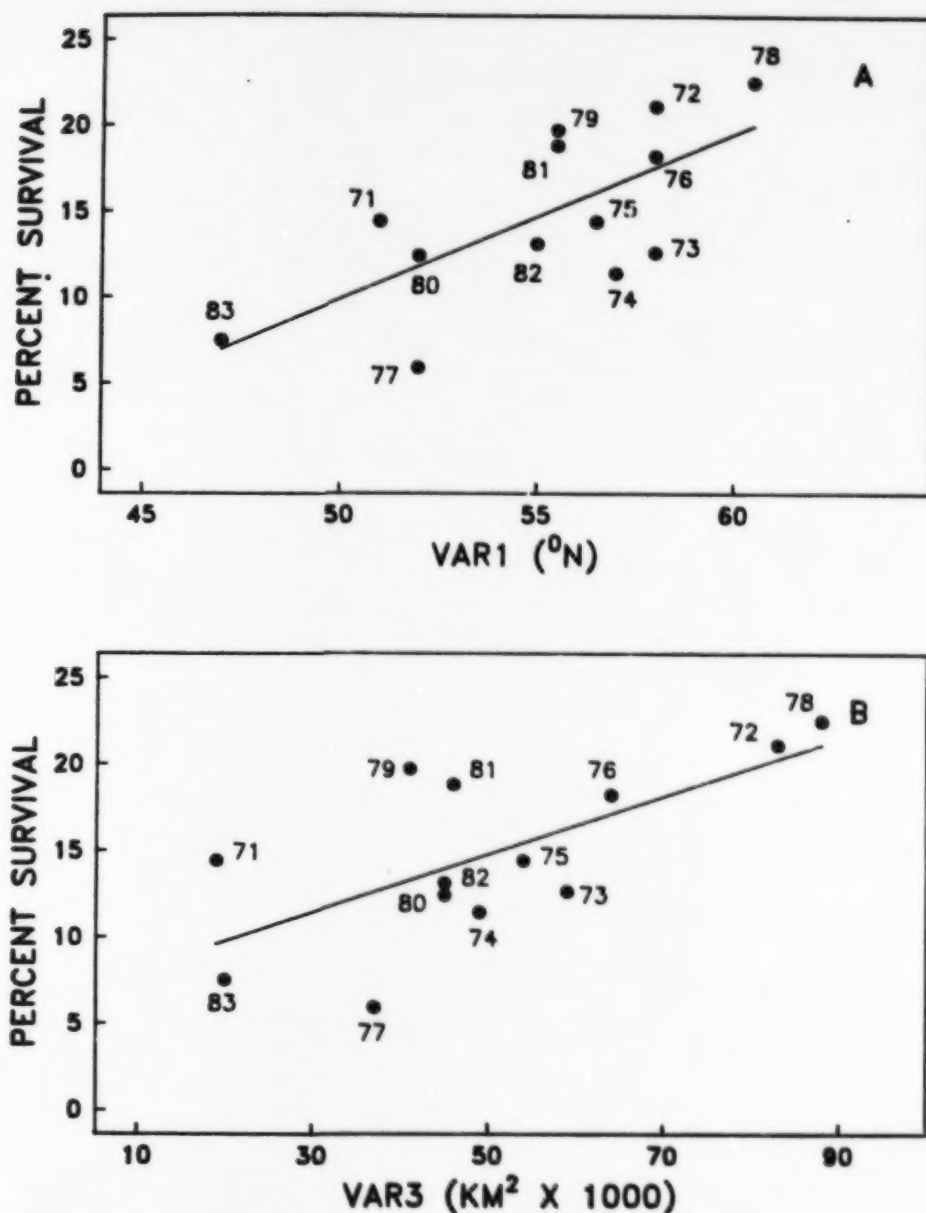


Fig. 5. Relationships between percent survival (expressed as number of recruits per 100 smolts) for smolts of Western Arm Brook and indices of winter SST conditions in the northwest Atlantic. A. Between percent survival and the latitude ($^{\circ}$ N) of northward extent in January of 4° C isotherm west of 45° W (VAR1). B. Between percent survival and the area ($\text{km}^2 \times 1000$) covered by 4° C or warmer water in January north of 50° N and west of 40° W (VAR3). Smolt year is identified with each point and lines were fitted by unweighted regressions.

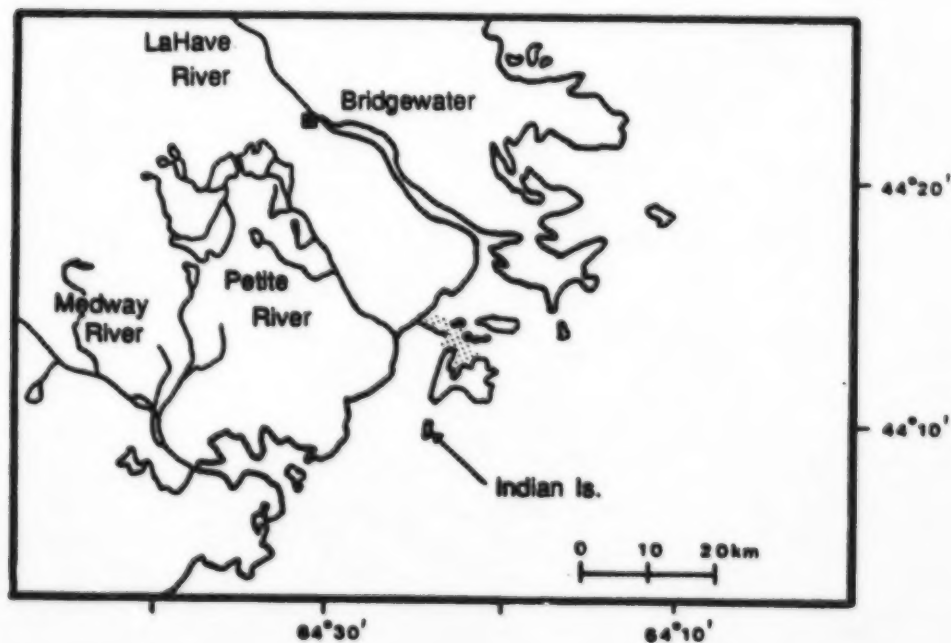
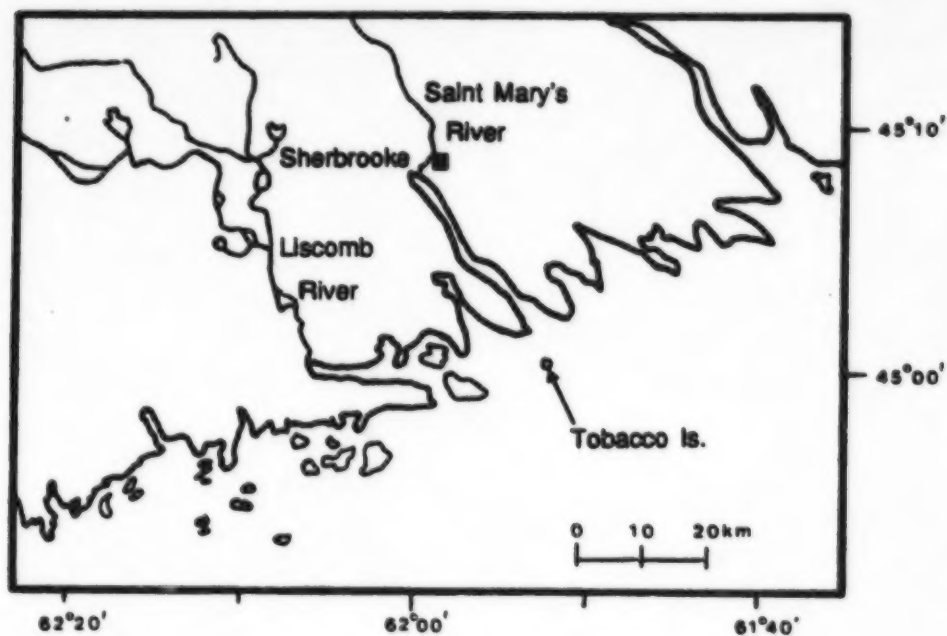


Fig. 6. Locations of Tobacco and Indian islands, the sites of two cormorant rookeries, and nearby rivers into which tagged hatchery smolts were released, 1981 to 1986.